VARIATIONS IN THE ACCUMULATION, DISTRIBUTION AND MOVEMENT OF MINERAL NUTRIENTS IN RADIATA PINE PLANTATIONS

by

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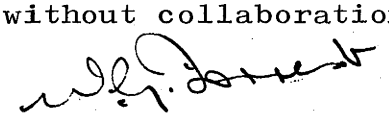
These papers constitute a thesis submitted for the degree of Doctor of Philosophy in the Australian National University.

ORIGINALITY OF THESIS

The collection of trees for the study reported in Chapter 1 of this thesis was assisted by the third and fourth year classes in the Department of Forestry of 1967, since it was essential that all material was collected and oven-dried as quickly as possible. Limited assistance was provided within the Department to help with the heavy manual work involved in sampling large trees (Chapter 2) and for some of the routine chemical analyses.

Most statistical analyses were made using multiple regression, linear regression and analysis of variance programmes available from several computer centres. Data processing has been done at the A.N.U. and C.S.I.R.O. computer centres with the help of Mr J. Armstrong of the Department of Forestry, and at the N.S.W. Public Service computer centre with the help of Dr B. Turner of the N.S.W. Forestry Commission. Mr J. Armstrong assisted in the preparation of other programmes for summarizing various data. Dr Turner and Dr N. Day of the A.N.U. have both given statistical advice.

With these exceptions, the work described in this thesis is original and was done without collaboration.



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ACKNOWLEDGEMENTS

The New South Wales Public Service Board, through the N.S.W. Forestry Commission, granted study leave for three years and financial assistance during the first two years of the study. The third year was supported with an Australian National University Research Scholarship.

Within the Department of Forestry, many staff members and fellow research students have shown interest in the project and their critical comments have been appreciated. Particularly I wish to thank my supervisor, Professor J. D. Ovington, for his continued co-operation, guidance and encouragement during the three years of study.

The N.S.W. Forestry Commission and the Department of Interior, A.C.T., gave permission for the destructive sampling and other operations within their plantations; Messrs R. Allen, R. Free and W. Bateman are thanked for their assistance.

Dr J. Fielding and Mr A. Brown of the Forest Research Institute, Canberra, agreed to the sampling within the field clone experiment, and gave helpful comment. Dr L. Pederick of the Victorian Forests Commission provided several batches of controlled- pollinated seed.

I am indebted to my parents for their encouragement, and above all, I am grateful to my wife and family for their continued support and encouragement during the past three years.

ABSTRACT

All trees within an area of 0.08 ha of Pinus radiata plantations were felled, dried and weighed. The results that would have been obtained using various sampling techniques for biomass estimation were compared against the known biomass in order to critically evaluate the accuracy of different procedures. Regression methods proved the most satisfactory and were used for all later studies.

The dry weights and nutrient contents of sample trees from several P. radiata plantations have been determined. From these values the production, accumulation and turnover of organic matter have been calculated for different stages of plantation development, as well as the corresponding values for six mineral nutrients, viz. phosphorus, calcium, potassium, magnesium, manganese and zinc.

Whilst the patterns of accumulation for the six nutrients varied, all accumulated most rapidly during the period immediately prior to canopy closure and it is suggested this time of greatest nutrient stress is critical in the tree:nutrient relationships. At this time the growth of the crown, which contains the greatest concentrations of nutrients, was at a maximum. The redistribution of nutrients within trees and plantation ecosystems are discussed and related to the results obtained by other investigators in order to indicate the significance of the various factors involved in nutrient flow.

Trees within a plantation differed markedly in the amounts of nutrients accumulated. From an investigation of the crowns of clonal trees, an indication of the relative importance of genotype and environment to variation in nutrient accumulation was obtained. The trees examined differed in nutrient content because of variation in crown structure and morphology and in the concentrations of

nutrients, all being under genetic control. Support for the conclusion that trees differ in nutrient requirements for optimal growth was obtained from a seedling glasshouse experiment.

The need for an appreciation of the tree's nutritional requirements is stressed and related to silvicultural practice.

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PART III

VARIATIONS IN THE ACCUMULATION, DISTRIBUTION AND MOVEMENT OF MINERAL NUTRIENTS IN RADIATA PINE PLANTATIONS

GENERAL INTRODUCTION

Plantations of exotic tree species for wood production were first established in Australia by forest authorities early in the present century, and by 1938 the area of plantations was about one - hundred thousand hectares. During the Second World War planting virtually ceased, and at the end of the war in 1945 the need to increase the area of exotic plantation was generally accepted.

The experience gained from the earlier plantings, then up to 30- years old, was invaluable as a guide to post-war developments. Plantations of radiata pine (Pinus radiata D.Don.) showed a higher growth rate than other species, exotic or native, particularly in the temperate zone. Increased growth resulting from fertilizer addition had also been demonstrated on many sites of poor natural soil fertility, and fertilizer applications had been shown to be justifiable economically.

By 1968 nearly three hundred thousand hectares of forest plantation had been established in Australia, of which about 70% was P. radiata and possibly 10% had been treated with inorganic fertilizers (notably superphosphate, but also zinc and potassium salts). The continuing extension of planting into new areas creates social, economic, silvicultural and administrative problems, and for many reasons it is desirable that the nation's forest produce be cropped from a minimum land area.

The rate of tree growth and wood production may be increased by site improvement, for example by fertilizer addition or drainage, by tree improvement through the

selection of fast growing species and of planting stock of superior quality, and by silvicultural improvement of the growing stands. In Australian forests the greatest production gains have been achieved when fertilizers have been used at sites of low natural fertility, and large differences in the intrinsic growth rate of trees in response to fertilizer addition have been demonstrated in many P. radiata plantations (Waring, 1962; Gentle and Humphreys, 1967; Raupach, 1967a).

Despite increased acceptance of the role of inorganic fertilizers in commercial forestry, and an improved understanding of the nutrient amendments neccesary on particular soil types, the relationships between the nutrient requirements of the tree, stand development and the genetic composition of forest stands are much less clearly understood, although these internal factors also influence both intrinsic growth rates and responses to fertilizer addition. The rapid growth of some forest stands and the consequent large uptake of nutrients from soils of low nutrient status could present serious nutritional problems, either in the first or in subsequent rotations.

Many studies of forest soil fertility have been concerned with the ability of the soil to supply essential nutrients, and only generalised estimates of the requirements of each nutrient for healthy tree growth have been considered. However, an awareness of the variation in nutrient accumulation and distribution both within and between forest stands will be necessary before optimum production can be obtained in problem areas.

The aim of this investigation is to examine the influence of some tree and stand characteristics, particularly of changes in tree development and of the genetic composition of the trees, on the mineral nutrient uptake by forest stands. Better knowledge of these influences and their interactions should permit a more

complete understanding of responses to fertilizer application in the field, and provide an improved scientific basis for applying the results of forest experiments to management practice.

Stand development is examined in Part I, so that in Part II, mineral nutrient accumulation and distribution, and the conditions under which nutrient stress is likely to be imposed, can be discussed. The chemical composition of individual trees within the stand, and between-tree variations in nutrient accumulation resulting from differences in morphology and physiology are examined in Part III. Finally, the significance of the data and the conclusions drawn to forest management are considered.

PART I

DRY MATTER ACCUMULATION IN PLANTATIONS OF *PINUS RADIATA*

CHAPTER 1

THEORY OF DRY MATTER ESTIMATION IN EVEN-AGED FOREST PLANTATIONS

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CHAPTER 1

THEORY OF DRY MATTER ESTIMATION IN EVEN-AGED FOREST PLANTATIONS

1.1 INTRODUCTION

The theory and practice of forest mensuration has been directed towards the accurate assessment of the commercially valuable part of the tree, i.e. usually the straight and substantial section of the bole suitable for processing into timber, pulp, etc. Normally bole length and/or diameter are measured and the volume is estimated from the measurements.

Quantitative estimates of other tree components or the total tree may be required for various purposes. For example, knowledge of the weight of the canopy foliage and branch wood may be important in watershed management, in investigations of tree growth and responses to thinning and other silvicultural treatments, in estimating quantities of forest fire fuels, in measuring food available to insects and other predators, and in studing growth and mineral nutrition of forest trees (Loomis, et al., 1966). Estimates of the amounts of non-woody parts may be required, e.g. of fruit, latex and cork. Dry weight is being used more generally as a measure of the tree components and in some situations is replacing volume as a measure of bole wood harvested.

In this investigation, the total tree and component dry weights have been determined primarily to calculate the total amounts of nutrients per tree and per unit area. The dry weight values are also discussed because the changing weight distribution with tree age greatly effects nutrient uptake and distribution.

Procedures for dry weight determination of most natural vegetation types of low structure and agricultural crops are well developed both in terms of sampling procedures and in sample handling. The weights of forest stands are difficult to assess because of the great mass of material present, and the morphological and structural diversity of forests causes sampling and statistical difficulties.

In many early studies (e.g. Ovington, 1957; Ovington and Madgwick, 1959a; Will, 1964) trees have been chosen to represent the stand, and stand dry weights have been derived by multiplication of the weights of these "mean" trees. This approach has been criticised (Baskerville, 1965b; Attiwill, 1966a) mainly because no estimate of precision can be calculated and underestimates are likely. Regression analysis techniques have also been used (e.g. Burger, 1929; 1936; 1940; Kittredge, 1944; Rutter, 1955; Baskerville, 1965a; Cable, 1958; Ovington and Madgwick, 1959a; Satoo, 1962), advantage being taken of the natural relationships existing between the readily measurable dimensions, such as bole diameter, and the weights of several components within a tree. Recently the technique has been subjected to limited critical examination (Weetman and Harland, 1964; Attiwill, 1966a; Attiwill and Ovington, 1968).

Where regression analysis has been used an allometric relationship has frequently been found between bole size and the respective component weight (for example, Kittredge, 1944; Ovington and Madgwick, 1959a; Satoo, 1962); for example the relationship:-

Log bole diameter = a + b Log foliage weight

has been determined for a number of widely contrasting tree species and a high level of statistical significance has been demonstrated. This allometric relationship was developed to describe the synchronous development of two unrelated variables within a single plant (Huxley, 1932),

is most reliable when the growth curves generated by the two variables are of a similar form (Dormer, 1965).

The frequency distributions of both size and weight variables for a forest stand result from the relative growth curve for those variables in each tree. When the near normal frequency distribution of size classes commonly found for plantation stands (Fig. 1.1) is expressed as a cumulative curve of increasing numbers of individuals with increasing size classes (Fig. 1.4a), the result is similar to the growth curve discussed by Winsor (1932) and Dormer (1965). The similarity in rate of development of several components within a tree and the consequent similarity in their frequency distributions is the basis for the reliability of the allometric equation.

Significant linear relationships of other forms have been developed for some stands, (Cummings, 1941; Rutter, 1955; Rogerson, 1964). Occasionally this may result from inadequate sampling; for example, although an allometric relationship exists for two variables of a population of trees, significant equations of the form:

$$\text{Log}_e \text{ weight} = a + b \times \text{D.B.H.}$$

could be derived if the upper size classes in the tree stand were not adequately sampled.

Canopy weight may be more closely related to bole diameter at crown break than at breast height (Attiwill, 1962) but this is not always the case (Loomis et. al., 1966), or may result from increased uniformity in bole configuration as well as for reasons previously proposed (Attiwill, 1962). Height has often been introduced with advantage, either with diameter (D.B.H. xHt.) as an expression of bole surface area, with basal area (B.A. xHt) as an expression of bole volume, or separately with one of these in a multivarate equation. Other variables such

as crown spread and depth have also been considered (Rogerson, 1964); rarely has their inclusion been of sufficient advantage to justify the difficulty of measurement, but this may have resulted from inadequate testing.

Despite the common use of regression analysis for describing relationships within forest stands and predicting stand weights, few studies have attempted to formalise the methodology, particularly that relating to sample selection and the sample size required to represent the population within predetermined confidence limits. This situation results largely from difficulty in defining the whole population (the forest stand) and of estimating the overall variability of the component weights.

A detailed examination of a single forest plantation was made so that both size and weight parameters were accurately known for each tree and so the several methods of forest stand weight estimation could be compared against the known stand weight.

1.2 COLLECTION OF DATA

1.2.1 The Forest Stand

The study plot was on a flat site in eight year old, unpruned, monoculture plantation of *P. radiata* and was typical of such plantations at Mt Stromlo. One year old seedlings had been planted in 1958 at three metre (10 ft) intervals along lines ripped two metres (7 ft) apart to give an initial stocking density of 1500 per hectare. Due to natural causes, probably drought, this stocking had decreased to about 1200 after eight years. The forest canopy had almost closed giving about 90% cover, the lowermost whorls of most trees were dead and the ground vegetation was sparse (Plate 1.1).

PLATE 1.1 Stromlo plantation, 100 - tree plot. Photo taken after removal of above - ground parts, and showing stumps prepared for root extraction. Trees shown adjoined and were similar to plot trees.

At the time of clear felling for weight determinations, the average tree height was 8 metres (26.2ft) and the average dry weight was just over 53 kilograms (Tables 1.1 and 1.2). Despite the uniformity of management over the area, the trees varied considerably in size, the largest was about four times the smallest in crown and bole linear dimensions. The comparable oven dry weight range was even greater being 87x, 131x, 52x, 54x, and 49x for leaves, living branches, bole, root and total tree respectively. In general the size frequency distributions of trees show a near normal, slightly skew distribution for the various size parameters (Fig. 1.1).

TABLE 1.1 Range of tree size (cm) in study plot of 100 trees

	Maximum	Minimum	Average
Tree height	1018	268	800
Crown depth to lowest living branch	994	256	760
Crown diameter	549	107	335
No. of living branches	154	29	78
No. of whorls with living branches	26	5	13
Bole diameter at ground level	20.9	5.8	16.8
Bole diameter just below lowest living branch	21.5	5.1	15.9
Bole diameter at breast height (130 cm)	21.6	3.9	13.0

The planting rows ran north to south and detailed comparisons of tree crown spread to the north, south, east and west of the boles revealed no consistent difference in development associated with orientation. Root examination suggested local soil conditions may determine tree size largely through their effects on root development. The soil varied locally from a medial red

FIG 1-1 TREE SIZE FREQUENCIES

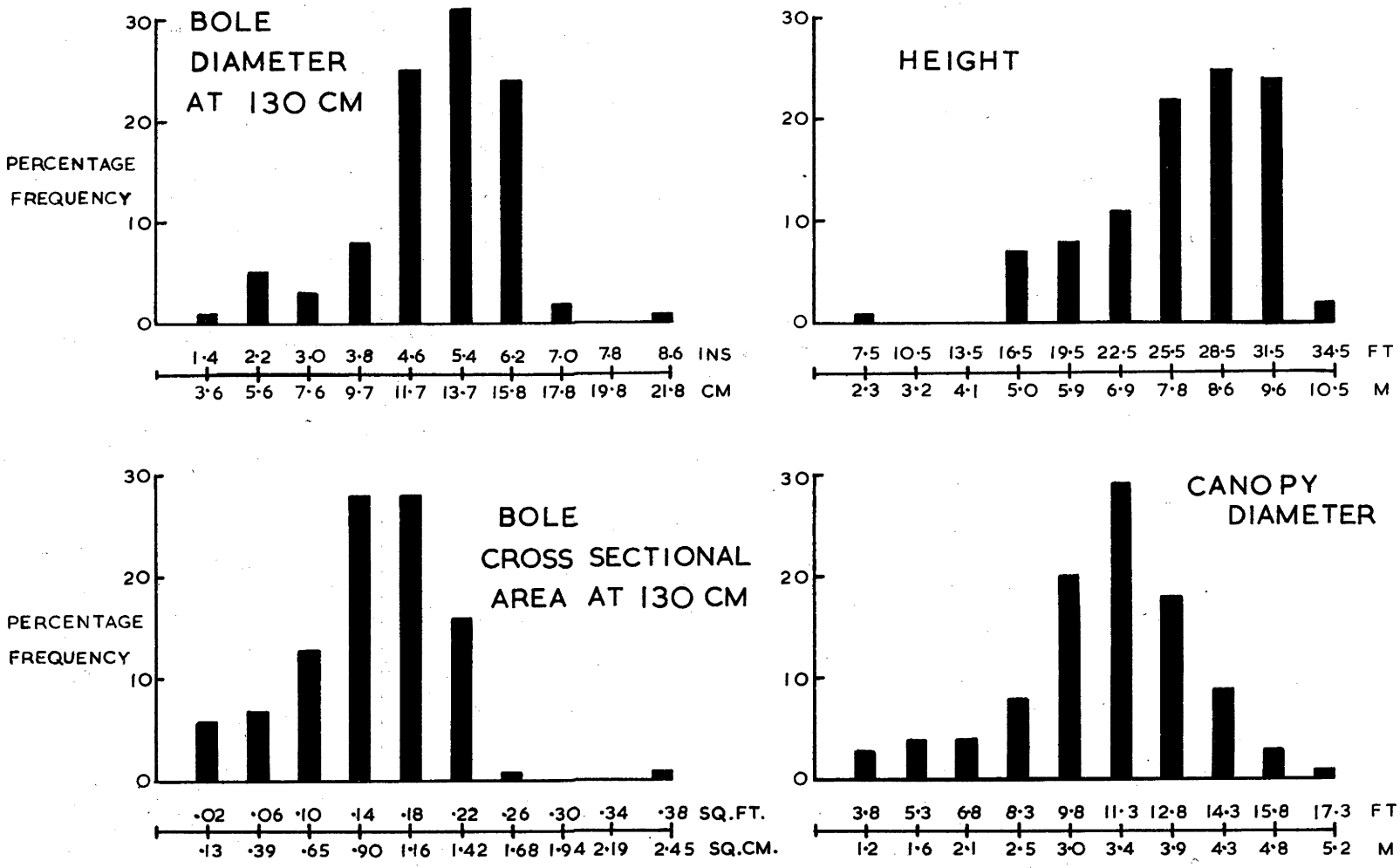


TABLE 1.2 Range of oven dry weights in study plot of 100-trees.

	Single trees (kilograms)			All trees (kilograms per hectare)
	Maximum	Minimum	Average	
Male Cones	1.42	0	0.22	277
Mature female cones	2.84	0	0.12	148
Immature female cones	0.06	0	0.01	10
Leaves	28.80	0.39	8.46	10,457
Living branches	50.66	0.39	13.63	16,840
Dead branches	3.31	0	0.84	1,040
Bole	40.94	0.85	21.62	26,709
Roots with diameter greater than 5mm	24.13	0.45	8.56	10,573
Total (exclusive of fine roots)	149.57	3.07	53.47	66,054

podzolic to a minimal yellow podzolic (Brewer, 1955). On the better aerated red soil with good permeability the trees had deep tap roots, sometimes several per tree, but elsewhere tap roots were poorly developed or absent, being replaced by a mass of finer roots. The large lateral roots were in the top 30 cm (12 ins) of soil.

1.2.2 Field and Laboratory Methods

A study plot of 0.081 ha (0.20 ac) was marked out in the extensive plantations of P. radiata at Mt Stromlo near Canberra, Australia. The plot contained one hundred living trees, the location of each tree was mapped and it's crown spread, height and bole diameter at breast height (130 cm, 4 ft. 3 in) measured. In September 1966 each tree trunk was severed at ground level and the tree carefully lowered onto a tarpaulin to minimise loss of tree parts. Additional trunk and crown measurements were made on the felled tree (Table 1.1).

Immediately after felling and measuring each tree, the oven dry weights of the component parts were determined as follows. All branches were cut from the bole and separated into living (i.e. with green leaves) and dead branches. The cones were picked from the branches and separated into male, current female and previous year female and placed in paper bags for oven drying. The remaining crown (leaves and branches) was cut into suitable lengths and placed in large paper bags. The trunk was sectioned in 1.5 metre (5 ft) lengths and transported with the full paper bags to the laboratory three kilometres (2 miles) away for oven drying.

The paper bags and their contents were dried to a constant weight in a large forced-air oven maintained at 85°C, crown material being stored in a cold room at 4°C until oven space was available. A preliminary trial (Appendix 1) showed temporary storage of plant samples in the cold room caused no appreciable change in dry weight. All crown drying was virtually completed within a week from tree felling, after which leaves were separated from branches, and the dried cones, leaves and branches were weighed as complete groups for each tree. Whilst the crowns were being oven dried, the bole sections were given a preliminary drying in a room heated to 60°C after which the entire bole sections were oven dried at 85°C and weighed.

Individual tree roots were extracted from the soil using a tractor winch and by hand digging. No attempt was made to collect fine roots but great care was taken to ensure all roots having a diameter greater than 5 mm were collected. After carefully brushing all soil off the roots they were cut into manageable pieces, over dried and weighed.

Since entire components of each tree were dried and weighed, the individual tree dry weights are believed to be

reasonably accurate, although they would be slight underestimates because of unavoidable loss of some kinds of organic matter. Pollen and male cones were lost during the felling and breakdown of the trees but this loss would be less than 0.1% of the total tree weight. Some bark flaked from the trunk and branches but again this would be a small proportion of the total weight.

1.3 RESULTS AND DISCUSSION

The tree data collected before and during harvesting of the sample plot, and the dry weights of trees by components are given in Appendices 2 and 3 respectively. The sample plot is in effect the total population, but is thought to be representative of the surrounding area. Estimates of stand weight derived by sampling theoretically within the population can be compared to the actual total population weight. Summation of the oven dry weights of all trees in the study plot gave a biomass of 66 thousand kilograms per hectare, the relative percentages of cones, leaves, branches, boles and roots being approximately 1, 16, 27, 40 and 16 respectively (Table 1.2).

1.3.1 Comparison of Sampling Methods

Three main types of sampling to determine the tree biomass of a plot were examined, namely

Unit Area

All tree material in a prism extending above and below a sample area, or series of sample areas, is collected and weighed. The tree biomass for the plot is determined by converting the sample area data to a plot area basis.

Average Tree

In this method a tree, or number of trees, considered to be of average biomass because they have average linear dimensions, are selected, ovendried and weighed. The tree

biomass for the plot is determined by multiplication of the weight of the sample tree (or average of the sample trees) by the number of trees in the plot.

Regression Analysis

A number of trees, selected either randomly or systematically, are dried and weighed and the mathematical relationship between the weights of the whole trees, or tree components, and one or more tree dimensions calculated. Knowing the relevant linear dimensions of all trees in the plot, the tree biomass for the plot is determined from the regression equation.

Typical dimensions used in average tree and regression analysis methods for weight determinations are tree height, crown volume and the diameter and cross sectional area of the trunk at various heights (Figs. 1.2, 1.3a, and 1.3b). Since the cross sectional area of the bole at breast height gave relatively satisfactory relationships and can be easily measured all results are given on this basis unless otherwise specified.

(a) Unit area methods

Unit area sampling was not done in the study plot since the destructive sampling would have prevented the summation of individual tree weights to obtain an accurate reference value for tree biomass per unit area. Knowing the location, weights and crown plans of individual trees, the distribution of organic matter as dry weight over the plot could be simulated on the computer. By scanning the plot model unit area methods could be applied to obtain estimates of tree biomass by various methods to compare with the known biomass value (Table 1.3a). In practice, greater errors occur in using clip sampling methods than those given since crown weight in the model was considered to be uniformly distributed over the crown plan of individual trees. Because of the large size and

FIG 1-2.- TOTAL DRY WEIGHT — TREE SIZE RELATIONSHIPS

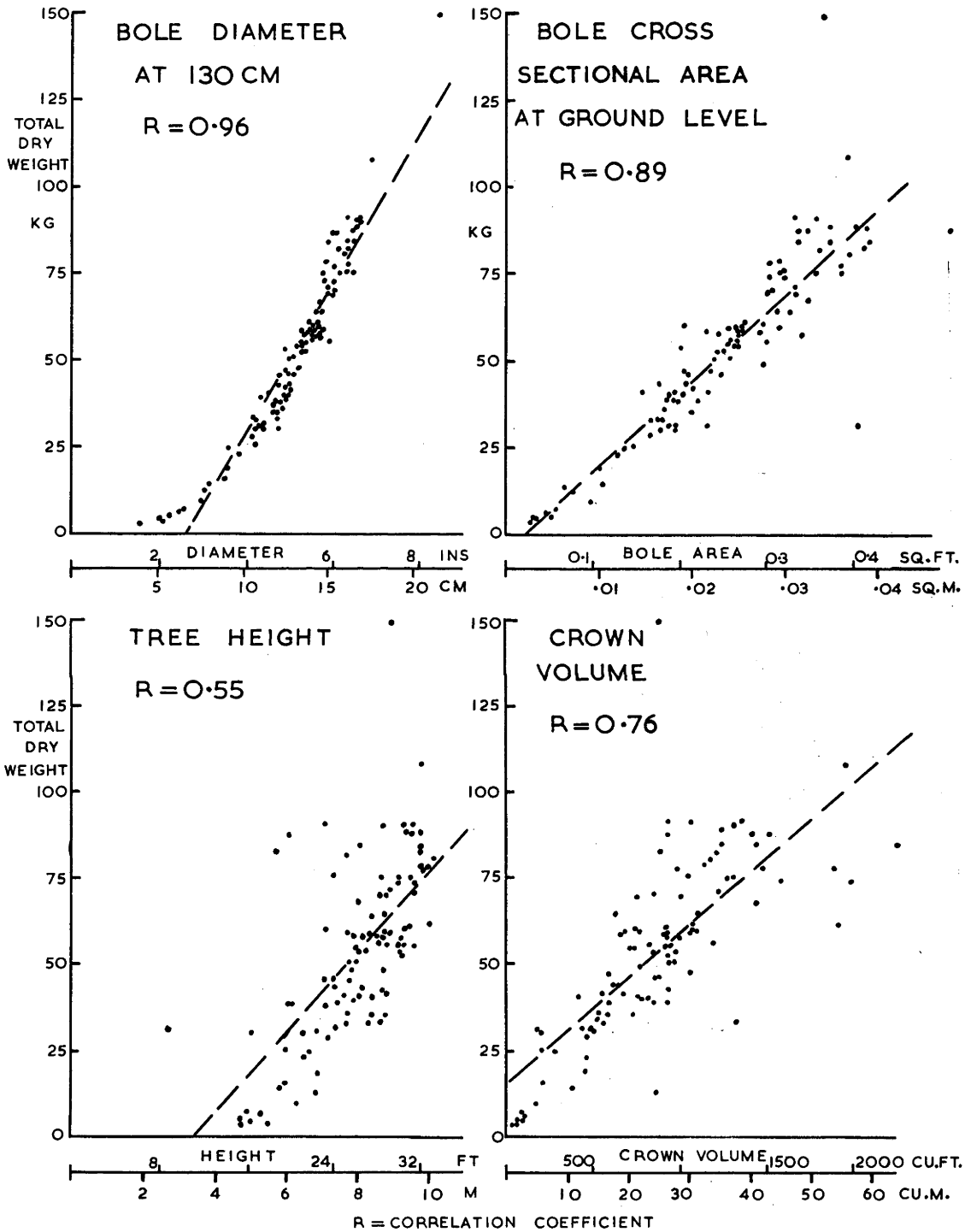
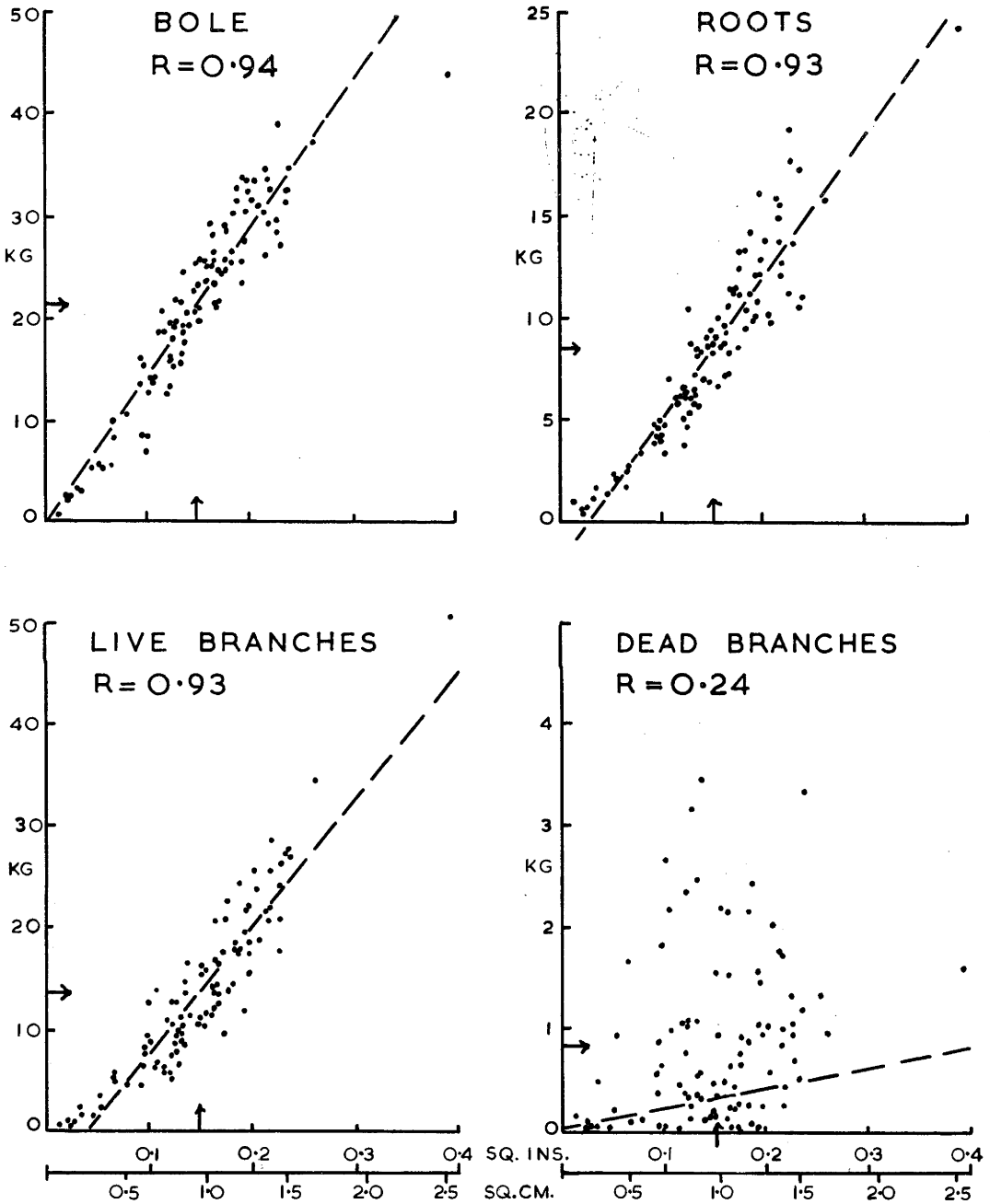


FIG. 1-3A

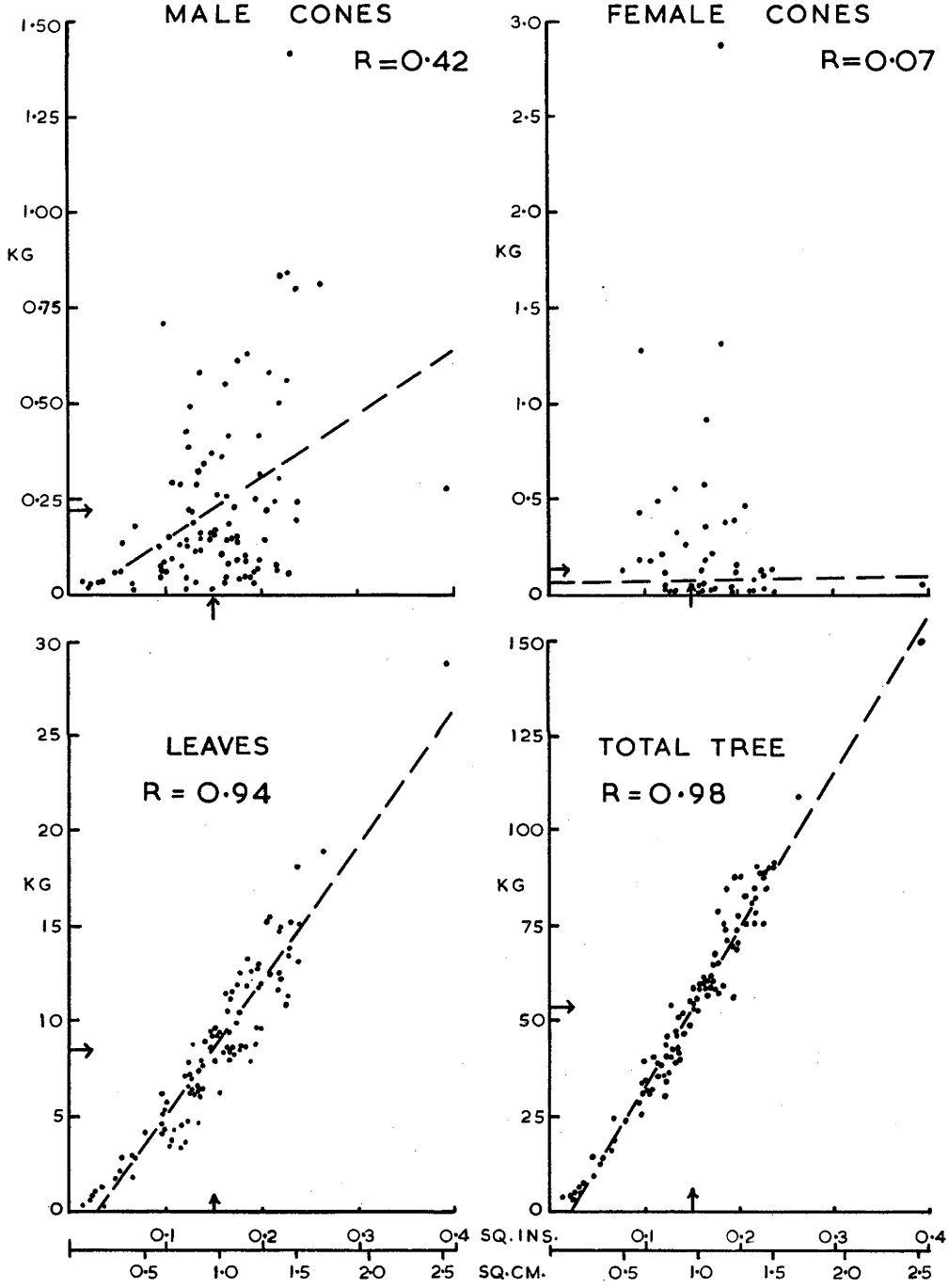
DRY WEIGHT — BOLE CROSS SECTIONAL AREA RELATIONSHIPS



BOLE CROSS SECTIONAL AREA AT 130 CM. ARROWS INDICATE AVERAGES. R=CORRELATION COEFFICIENT.

FIG. 1-3 B

DRY WEIGHT — BOLE CROSS SECTIONAL AREA RELATIONSHIPS



BOLE CROSS SECTIONAL AREA AT 130 CM. ARROWS INDICATE AVERAGES. R = CORRELATION COEFFICIENT.

TABLE 1.3a Percentage errors in stand oven dry weight estimates using unit area methods

Five random square plots

Size of each sample square (sq.m)	0.84		3.34		7.53		13.38	
% of area sampled	0.5		2.1		4.7		8.3	
Grade	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate
Canopy	-4	-46	-12	-36	-2	-29	-11	27
Bole	-100	1402	-60	-100	-1	-100	9	-100
Total	-25	673	-35	-66	1	-61	1	-54

Ten random square plots

Size of each sample square (sq.m)	0.84		3.34		7.53		13.38	
% of area sampled	1.0		4.2		9.4		16.6	
Grade	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate
Canopy	8	100	7	60	-1	-32	2	92
Bole	-100	1205	-39	146	24	-100	9	105
Total	-11	584	12	72	-4	-65	8	94

TABLE 1.3b Percentage errors in stand oven dry weight estimates using unit area methods

Size of each sample square (sq.m)	0.84		3.34		7.53		13.38	
Maximum possible number of samples based on a square grid of 0.1 sq.m.	8346		7800		7272		6762	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Canopy	329	-100	282	-100	262	-94	195	-81
Bole	1869	-100	392	-100	241	-100	204	-100

complexity of forest ecosystems, further error might be introduced due to practical difficulties associated with accurate outdoor colection of material above and below unit area.

Estimates of canopy weight per unit area proved more accurate than corresponding bole estimates largely because the crowns cover about 90% of the plot area whereas boles only occupy about 0.3%. For example, all 15 random squares of 3.34 sq m (36 sq ft) area contained some crown material whereas only eight included bole material. Generally, increasing the number and area of the sample units reduces the percentage error but even for the most intensive sampling used, i.e. when almost 17% of the area was sampled, the average percentage error for total biomass for the ten random squares combined was 7%. When all possible unit areas over the study plot were considered using a model with a grid of 0.09 sq m (1 sq ft) for the four sample unit sizes, overestimates for bole and canopy were as high as 1869% and 329% respectively and underestimates 100% i.e. with no bole or canopy material present in a unit area (Table 1.3b). The percentage errors for individual components such as cones, leaves and branches would probably be even greater.

Accurate clip sampling under outdoor conditions is very laborious and time consuming and unit area methods of determining plant biomass in forests appear to be inaccurate and inefficient when compared with other methods described later. The use of vertical enclosures in forests to determine community photosynthesis or transpiration on a stand area basis presumably would give equally erroneous results due to the problem of obtaining a suitable unit area. Increased efficiency might result if the sample squares could be located on the basis of biomass distribution rather than at random.

(b) Average tree methods

Average tree methods assume it is possible to select a tree, or trees, which approximates to the average for all trees in total and component dry weights. The tree(s) may be selected by subjective sampling of trees of known dimensions or by objective sampling from the whole population e.g. by systematic sampling.

As an example of systematic sampling, all possible combinations of the weights of either every fifth, tenth or twentieth tree in the plot were grouped and averaged for each combination. The averages were multiplied by the number of trees in the stand to give the total biomass (Table 1.4a). The results, expressed as percentage errors of the known stand weights, descreased with increasing numbers of weighed trees but even with a 20% sample large errors (over 10%) occurred.

To improve the previous procedure, the average ratio of dry weight to bole cross sectional area at breast height was calculated for every combination group and multiplied by the total bole cross sectional area of the stand. This adjustment compensated for samples having exceptionally large or small cross sectional areas relative to the stand average and resulted in a marked improvement in the accuracy of estimated stand weights (Table 1.4b).

A different average tree approach is to try to select a tree or trees having dry weight distribution values corresponding to the stand average. No single tree in the study plot exactly met this requirement for all tree components. In order to select the trees most approaching this ideal, cross sectional bole area at breast height was used as the basis for selection.

TABLE 1.4a Percentage errors in stand dry weight estimates using average tree(s) methods.

Systematic sampling

Method	Every twentieth tree			Every tenth tree			Every fifth tree		
Number of trees averaged per group	5			10			20		
Possible number of combinations	20			10			5		
Grade	Most accurate	Least accurate	Average	Most accurate	Least accurate	Average	Most accurate	Least accurate	Average
Male cones	-0.1	101	32	-4	33	19	-4	33	15
Female cones	3.4	388	90	-5	161	70	31	-82	62
Leaves	-1	51	21	-1	33	14	5	-18	11
Live branches	2	-40	22	1	37	17	4	22	14
Dead branches	-1	-72	26	1	52	25	6	29	20
Boles	-1	-47	21	-4	-28	16	3	-20	12
Roots	1	59	26	-3	-34	21	-1	-34	14
Total Trees	0.4	-44	21	-4	32	17	3	-20	12

Average percentage errors estimated by disregarding algebraic sign.

TABLE 1.4b Percentage errors in stand oven dry weight estimates using average tree(s) methods

Systematic sampling with proportionate adjustment to stand bole cross sectional area

Method	Every twentieth tree			Every tenth tree			Every fifth tree		
Number of trees averaged per group	5			10			20		
Possible number of combinations	20			10			5		
Grade	Most accurate	Least accurate	Average	Most accurate	Least accurate	Average	Most accurate	Least accurate	Average
Male cones	1	72	27	-1	28	11	-1	14	6
Female cones	6	395	88	-10	148	68	23	-82	58
Leaves	0.3	16	6	0.5	10	4	0.3	5	2
Living branches	0.4	-24	6	-0.3	-14	6	2	-8	5
Dead branches	-0.1	71	31	8	45	28	-8	-32	16
Boles	0.2	-13	5	0.1	-9	4	0.1	-5	3
Roots	2	-29	9	3	-17	7	-1	-8	5
Total trees	1	10	5	0.2	-9	4	2	-5	3

Average percentage errors estimated by disregarding algebraic signs.

TABLE 1.4c Percentage errors in stand oven dry weight estimates using average tree methods

Sampling around the tree of average bole cross sectional area

Method	Trees closest to average bole cross sectional area					Trees closest to average for bole cross sectional area, height, crown diameter and depth graded equally	
Number of trees averaged	1	2	5	10	20	1	2
Male cones	-94	-63	-23	8	-6	-30	18
Female cones	-100	-100	-100	-78	-62	-99	-100
Leaves	9	11	7	2	-0.1	9	10
Living branches	-22	-5	0.5	-3	-7	11	-4
Dead branches	-44	19	-37	-23	-14	-60	-69
Boles	17	12	2	5	4	-3	-3
Roots	10	6	-1	-2	-3	-2	-10
Total trees	3	6	1	1	1	1	-3

The component weights of the tree of nearest average bole cross sectional area, and the average weights of groups of trees having bole cross sectional areas closest to this tree, were multiplied by the total number of trees per unit area to determine biomass and the percentage errors against the known biomass (Table 1.4c). Repeating the procedure for trees with smaller or larger boles than the average gave no improvement in accuracy. For corresponding numbers of sample trees, sampling around the average tree generally gave better results than systematic sampling. However, estimates of the weight of components such as male cones, female cones and dead branches based on average trees were much more inaccurate, the weights of these components not being related to bole cross sectional area. In fact none of the five trees closest to the average carried any female cones. Since cones and dead branches represent only a very samll proportion of tree weight, the percentage error for the stand biomass is nevertheless reasonably accurate. Where accurate cone and dead branch weights are required, it would seem better to estimate these components separately using some systematic sampling of only those trees carrying cones or dead branches respectively.

In some situations average tree sampling might have to be restricted to one or two trees. Bole cross sectional area, tree height, crown diameter and crown depth were considered together and given equal ranking to test if this improved tree selection for weight estimates with a limited number of sample trees. Combining these characters in this way gave a remarkable improvement in biomass estimates for one tree sampling although errors in cone and dead branch estimates remained considerable.

(c) Regression analysis methods

Regression analysis methods assume for the population a relationship between total tree or tree component weights and some other easily measured parameter or combination of

parameters. Whilst major tree components are related linearly to the parameter adopted in this study, namely bole cross sectional area at breast height, no significant relationship existed for minor components such as cones and dead branches (Figs. 1.3a and 1.3b). Consequently, relatively large errors were obtained for estimates of the weight of the minor components but these, because of their small proportionate representation, had little effect on total biomass estimates. It should be emphasised regression equations of high significance could be derived by chance for particular sets of sample trees which if used to estimate the weights of the whole population would give very incorrect estimates of stand weight (Figs. 1.2 and 1.3).

Under certain circumstances, biomass determination by destructive tree sampling may be restricted to certain trees within a stand, for example the largest trees, the smallest trees, the average trees or some combination of average, large and small trees. When sampling is restricted to trees from a very small group of the population, regression analysis methods are not particularly appropriate and may give large errors (Table 1.5a).

Sampling based on the five largest trees, which contain 10% of the stand weight, gave more accurate estimates than those based on the smallest trees, 0.5% of the stand weight, because the largest trees extend over a greater size range and are more representative of the stand biomass. For this study plot and the various kinds of restricted selection examined, regression analysis gave the most accurate results when based on the group of trees around the average, extending the sample spread about the average by including more than the five trees gave little improvement in accuracy.

TABLE 1.5a Percentage errors in stand oven dry weight estimates using regression analysis methods

Restricted choice of trees based on bole cross sectional area

Method	Smallest tree	Largest tree	The smallest and the largest tree, and three trees closest to average	Trees closest to average		
Number of trees used	5	5	5	5	10	20
Male cones	-101	168	35	-18	8	-10
Female cones	-100	-76	95	-100	-76	-68
Leaves	-21	-2	12	8	3	2
Living branches	-70	13	22	-3	-6	-4
Dead branches	-151	69	-20	-41	-22	3
Boles	-22	28	-10	3	5	5
Roots	-77	-17	4	-2	-3	-3
Total trees	-45	13	3	0.2	0	0.7

TABLE 1.5b Percentage errors in stand oven dry weight estimates using regression analysis methods

Subjective tree selection within strata over the whole population range

Method	Average tree in each of 5 equal number classes	Average tree in each of 10 equal number classes	Average tree in each of 5 equal size classes	Average tree in each of 10 equal size classes
Number of trees used	5	10	5	10
Male cones	25	51	6	57
Female cones	-21	-60	-91	172
Leaves	-5	-3	16	10
Living branches	5	7	20	23
Dead branches	-20	11	-42	-17
Boles	-2	-3	1	-6
Roots	-5	4	-6	2
Total trees	-1	1	6	6

TABLE 1.5c Percentage errors in stand oven dry weight estimates using regression analysis methods

Random selection of trees

Method	Random trees in whole population		Random tree in each of 5 equal number classes covering whole population		Random tree in each of 5 equal size classes covering whole population	
Number of random regressions	10		10		10	
Number of trees per regression	5		5		5	
Grade	Most accurate	Least accurate	Most accurate	Least accurate	Most accurate	Least accurate
Male cones	-1	102	-16	88	-2	102
Female cones	-16	627	-7	375	-36	-100
Leaves	-1	29	4	15	-0.3	20
Living branches	-1	-18	1	9	1	21
Dead branches	3	-77	-1	89	-3	59
Boles	3	-10	-1	8	1	-11
Roots	1	25	2	21	1	-17
Total trees	0.1	10	1	7	0.1	3

In order to obtain a better distribution of sample trees over the population for regression analysis, the whole population was divided into five or ten equal tree number or size classes and the sample trees were selected as being the nearest to the average of each class (Table 1.5b). Apart from cones and dead branches the biomass estimates were reasonably accurate, tree classification by numbers being superior to that by size and no great improvement in accuracy was obtained by increasing the number of sample trees from 5 to 10.

Where trees are selected randomly from the population for regression analysis the potential error is considerable even though the probability of obtaining the greatest possible percentage error is small (Table 1.5c). Percentage errors for the most accurate and least accurate results for ten random regression lines each based on five trees are given for random sampling in the whole population and for stratified random sampling according to number or size classes of trees. Of these two kinds of regression analysis methods stratified sampling seems the more reliable.

1.3.2 Further examination of regression analysis methods

(a) Nature of relationships existing in population

The relationships existing between several tree size and weight variables should be examined for the whole population, since the goodness-of-fit of such total population relationships determines the reliability and probable significance of comparable equations derived from a sample of the population.

When the equation $Y = a + bX$ is calculated for all values of the tree variables X and Y, then $\hat{Y}$ (i.e. the estimate of total weight) can be calculated by solving the equation for all values of the independent size variable, X; $\hat{Y}$ is then seen to be equal to the actual stand total Y, but will have confidence limits defined

by the residual mean squares of that regression. Unless the confidence limits of the total population regression are small in comparison with total Y, estimates of Y from sample based regressions cannot be reliable, even though the confidence limits of the sample regression may fortuitously be small.

Some relationships between total tree and component weight and bole size for the population detailed in Appendices 2 and 3 are shown in Figs. 1.2 and 1.3. The value, for stand weight prediction, of the regression equations resulting from these and similar relationships can be compared in Tables 1.6 and 1.7. Dry weights of the major components and total dry weights are closely correlated with each of the size parameters listed, both directly and after log: log transformation. While there appears to be broad relationships between both male cone weight and weight of dead branches with bole size, these relationships are not close compared with those for the major components, and there is virtually no relationship for female cones. Both male cone and female cone production are considerably influenced by genetic differences among trees but cone production in a P. radiata stand is also normally correlated with bole size (Fielding, 1960). The lack of correlation in this plantation stand must be attributed to the stand's youth; male flowering and female cone production commence at about 3 years and 4 years of age respectively (Fielding, 1960), and without strong competition genetic factors are probably most predominant. Similarly, dead branch weight probably becomes more closely correlated with bole size as competition between trees increases with greater age. Unless there are significant relationships with bole size, minor components should be estimated from select populations; for example, sampling may be confined to trees bearing the particular component and precision estimates calculated

from the variance of the sample distribution. However, these minor components usually contribute a small part of the total dry weight and a low level of precision may be tolerable.

For the one hundred trees crown component dry weights are correlated less with bole volume and bole surface area than with basal area and diameter. The effect of height may increase as crown dominance patterns become more definite with increasing age. The allometric relationships are all more significant than the comparable direct untransformed relationships, but less than would appear from the T-values listed in Tables 1.6 and 1.7. For any of the regression equations of total tree weight against the bole size variables listed in Table 1.6, the range of confidence limits ($P = 0.01$) for estimated total stand weight is less than 1% of the actual total stand weight.

The factors leading to the significance of the allometric relationships are discussed previously (page 8), and the conclusions made are confirmed by reference to the several size and weight accumulative frequency distributions shown in Figs. 1.4 and 1.5. The degree of correlation between size and weight variables is directly related to the degree of similarity between their frequency distributions.

Given highly significant linear relationships between tree size and weight variables, further improvement could only be achieved by including other measurements of tree size, such as canopy spread and depth, through a reduction in dispersion of points from the regression line, with consequent reduction in residual mean squares. No such reduction occurs for this population (Fig. 1.2), and this is substantiated by multiple regression analyses which include these other variables. Measurement of the bole

TABLE 1.6 Significance of linear relationships between bole size and tree weights for population of 100 trees

T- values = $b/S.E._b$ For significance (P=0.01) , T = 2.63.

Independent Variable	Dependent Variable (Dry Weights)							
	Bole	Branches	Leaves	Roots	Dead Branches	Male Cones	Female Cones	Total Tree
Diameter B.H.	29.81	18.02	20.93	21.02	2.44	4.44	0.91	31.81
Basal Area	28.42	24.08	28.15	25.19	2.39	4.56	0.71	48.59
Diam. at Crown Break	18.75	14.47	15.71	18.73				20.17
Diam. at Ground	19.54	13.07	13.76	16.14				18.72
Sec. Area at Crown Break	17.55	16.10	17.09	21.47				21.45
Sec. Area at Ground	18.50	14.15	14.38	17.45				19.54
D.B.H. x Ht.	28.04	12.23	15.96	17.15				20.87
B.A. x Ht.	29.73	17.31	22.32	21.96				31.44

TABLE 1.7 Significance of various allometric relationships between bole size and tree weights for population of 100 trees.

$(\text{Log}_e Y = a + b \text{ Log}_e X)$ T - values = $b/\text{S.E.}_b$

For significance (P = 0.01), T = 2.63

Independent variable	Dependent variable — Log_e dry weight.				
Log_e X	Bole	Branches	Leaves	Roots	Total tree
Diameter B.H.	45.69	31.91	32.87	33.68	67.01
Diam. at crown break	27.84	29.87	27.05	30.62	37.58
D.B.H. x Ht.	32.95	17.39	22.40	23.18	27.04
B.A. x Ht.	47.78	22.42	28.46	29.59	40.98

at ground level or at crown break for this population gives less reliable relationships with component weights than measurement at breast height.

(b) Size and selection of sample

The reliability of the sample regression equation,

Y (weight) = a + bX (size)

is determined by the extend to which the sample represents the population; the statistical precision of an estimate of total population weight ($\hat{Y}$) based on that equation is determined from the variance (ω^2) of the regression where:

$$\omega^2 = \delta^2 \left(\frac{N^2}{n} + \frac{[\sum(X - \bar{x})]}{\sum x^2}\right) \qquad \text{equation 1}$$

where N = number in population

n = number in sample

X = values of size variable in population

$\bar{x}$ = sample mean

$\sum x^2$ = corrected sum of squares for sample

δ^2 = residual mean square of regression

FIG. 1-4 CUMULATIVE FREQUENCY DISTRIBUTIONS OF BOLE SIZE PARAMETERS FOR TREES IN 100-TREE PLOT

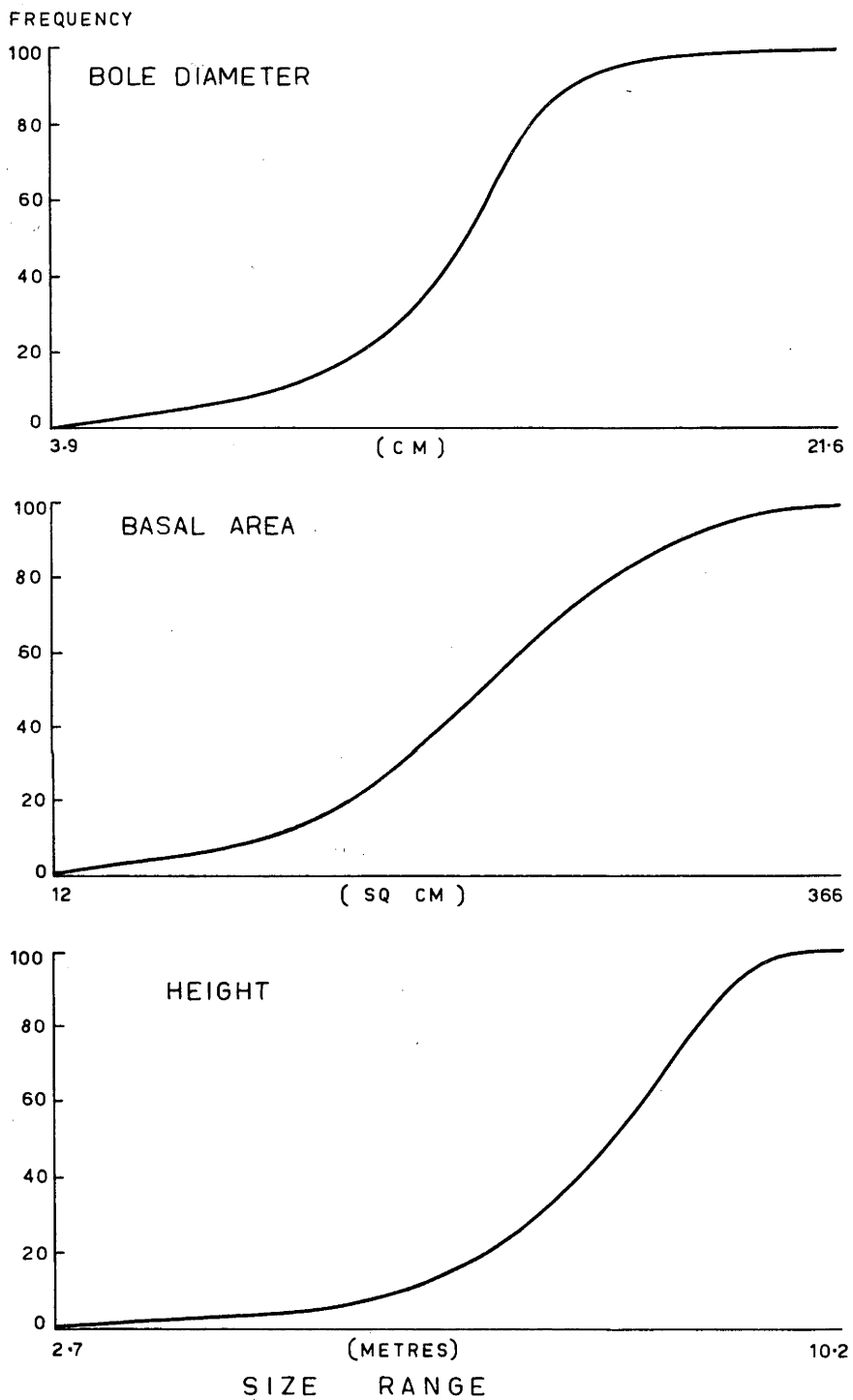
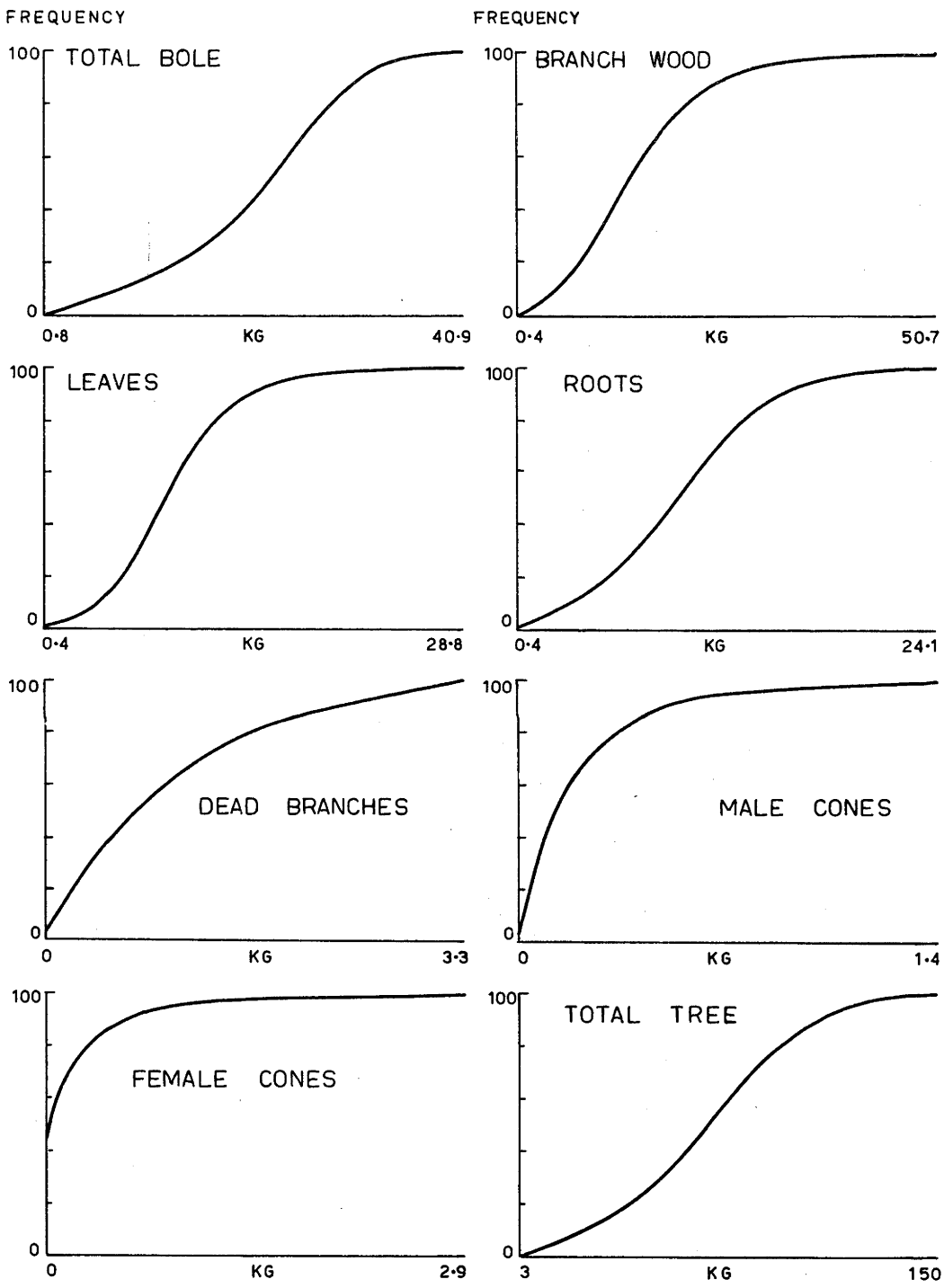


FIG. 1-5 CUMULATIVE FREQUENCY DISTRIBUTIONS OF COMPONENT WEIGHTS FOR TREES IN 100-TREE PLOT



Both practical reliability and statistical precision must be considered in sample selection.

Because δ (sample) is determined largely by δ (population), the variance (ω^2) of a regression can be decreased by

(i) increasing n
(ii) increasing Σx^2
(iii) decreasing $\Sigma(X - \bar{x})$

$\Sigma(X - \bar{x})$ will be small when the sample mean ($\bar{x}$) approaches the population mean ($\bar{X}$), and then the expression

$\left[\frac{\Sigma(X - \bar{x})}{\Sigma x^2}\right]^2$ is usually insignificant.

Sampling is usually subjective within the range of the independent variable X, provided for a given value of X the selection of values of the dependent variable Y is random (Snedecor, 1956; Jeffers, 1960). Thus a representative sample can be assured by subdivision of the range of X into classes of equal numbers, and selecting equally from each class; selection should be made with reference only to the X variable, since the introduction of other considerations could introduce bias; for example, where the sample and subsequent regression equation is to be based on bole basal area, sample selection within basal area classes of trees showing average crown size may introduce consistent bias.

The number of trees to be chosen, and the number of classes from which to draw the sample will depend on the variability of the population. Where a significant relationship exists between size and weight, a sample will most reliably describe that relationship when drawn from the full range of the size variables and with minimum deviation from the population regression line (Fig. 1.3).

Maximum deviation of the estimated total ($\hat{Y}$) from the actual total (Y) will occur when each sample tree by chance occupies the extreme position from the mean of it's class and is consistently to one side of the regression line. The probability of such selection occurring is $1/n^m$, where n = number of trees in class

and m = number of classes

and this probability is minimised when n^m is maximum, i.e. when n = 3.33. In the usual forest stand to be sampled subdivision into size classes of 3.3 trees per class would give more classes than trees to be sampled; however the extension of this reasoning indicates the desirability of subdividing the population so one sample tree can be drawn from each class.

The sample size required to satisfy predetermined precision limits will depend on the variability in values of Y for given values of X, i.e. on the regression variance.

The limits of Y are given by $\pm \frac{t.\omega}{n}$

where t is the appropriate T-value for (n-1) degrees of freedom.

n = sample size,

and $\omega = \sqrt{\text{variance}}$ as defined in equation 1

Assuming the sample variance will approximate the population variance and the sample mean will approximate the population mean, then in the population of 100- trees being examined the following numbers of trees would be required to obtain the significant regression equation: -

weight = a + b Basal area

with confidence limits = 5% of actual stand weight.

Components	Approximate number of trees required in sample
Bole	6
Branches	10
Needles	7
Roots	8
Dead branches	36
Male cones	40
Female cones	100
Total	4

In this population of 100 trees the major components and total stand weights can be reliably estimated from a sample of 10 trees; but the minor components cannot be satisfactorily estimated by this method, as indicated previously. The difference between the variances for direct linear regressions and allometric regressions of weight on bole size are not great, probably because the trees are relatively small. However, when a sample is drawn from a relatively unknown population regression equations to describe the weight: size relationships of the major components and total tree should be of the allometric form. Similar calculations to those above, although considerably more complex, would result in similar conclusions concerning size and selection of samples for allometric regressions.

1.4 CONCLUSIONS

Unit area methods are generally unsatisfactory for estimating tree dry weights in even-aged forest stands. Average tree methods are more satisfactory and, when the sample trees are selected carefully, may give very accurate estimates of component and total tree dry weights; however average tree methods are unsatisfactory in many studies

because precision of the estimate cannot be determined. Average tree methods can be used most appropriately in situations where damage and tree removal must be strictly limited, as in experimental plots.

In most studies where estimates of dry weights are required by components, the major component and total weights are best obtained from regression analysis. In young stands significant direct relationships between bole size and component weight may be expected, but in stands of larger trees with a wider range of weight values log: log transformations are most appropriate. Stands of even-aged monocultures, such as the one examined, can be adequately represented by about 10 trees selected from the range of size classes; the precision of the estimate should then be sufficient to allow comparison of silvicultural treatments, assess responses to fertilizer addition, and assess such other factors as nutient distribution. Minor components can probably be best assessed by other methods, particularly identifying those trees with and without the particular component.

CHAPTER 2

THE ACCUMULATION AND DISTRIBUTION OF DRY MATTER WITHIN A PINE STAND

Contents

CHAPTER 2

THE ACCUMULATION AND DISTRIBUTION OF DRY MATTER WITHIN A PINE STAND

2.1 INTRODUCTION

Our knowledge of the physiological processes which take place in forest trees is increasing, and providing a better scientific basis for silvicultural operations, particularly those aimed at increasing the productivity of forests. Much of this knowledge can only be applied to improving forest practice through an understanding of growth within all of the trees components, but particularly in the crown, "...but, it seems that foresters have regarded the foliage not so highly as the stems" (Tadaki, 1966).

A main objective of this investigation is to examine the effects of progressive stand development with age on the rate of uptake of mineral nutrients by P. radiata stands. As a basis for nutrient studies, data are required of the amounts and distribution of dry weight within a stand over successive periods through its development.

Ideally, data of the accumulation of organic matter and nutrients in forests should be based on records obtained over a complete rotation for individual stands. Since the investigation was limited to three years it was decided to study an age sequence of stands in a forest where site and environment were reasonably uniform so that the series could be regarded as representing the development of an individual stand. The study reported in Chapter 1 was carried out to provide a theoretical background to the analysis of the data to be collected in stands through the age series.

Plantations of P. radiata of various ages were examined in the Australian Capital Territory. Unfortunately the site

quality of these varied greatly between plantings of successive years and no acceptable age sequence could be obtained. The plantations in the Tumut region, some 50 kilometres (30 miles) west of Canberra were therefore examined. These have a more uniform site quality and a reasonable age sequence was selected in the Billapaloola Plantation. The site quality there was good (South Australia site index III) and appreciably better than that of the A.C.T. forests.

2.2 THE STUDY AREA AND SAMPLING METHODS

2.2.1 Location of study plots

Billapaloola Plantation, established and administered by the New South Wales Forestry Commission is 25 kilometres (16 miles) north - east of Tumut. Located between the Tumut, Murrumbidgee and Goodradigbee valleys, it is on a dissected plateau between 670 - 910 m (2200 - 3000 ft) altitude.

In April 1966 five stands planted in 1954, 1957, 1959, 1961 and 1963 were selected for study along the eastern aspect of a prominent north - south ridge running centrally through the plantation (Fig. 2.1). Comparable stands older than 12 years were not available, but this sequence extended well beyond the time of canopy closure. One study plot was carefully marked out within each of the five stands, care being taken to ensure aspect, slope, position on topography, soil development, original vegetation, stand history and stand development were as similar as possible.

2.2.2 Structure of the study plots

The initial aim was to establish circular plots of 0.101 hectares (0.25 acres), but because gaps occurred in most stands it proved impossible to always select large plots of uniform stocking density both within and between plots and with similar conditions in the immediate surrounds. Consequently for two plots (No. 2,1957 and No. 3,1959) the plot area was reduc

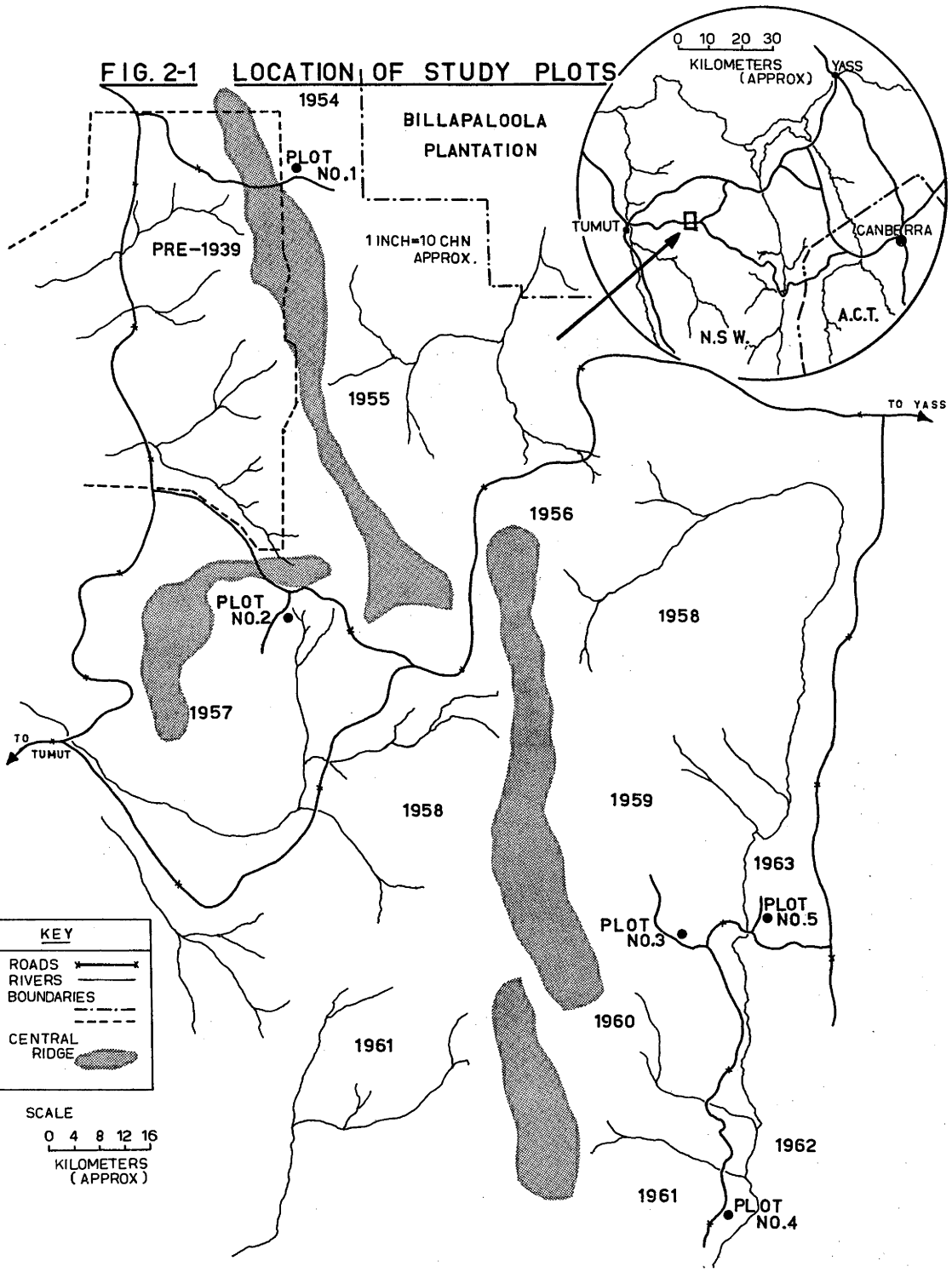


FIG. 2-1 LOCATION OF STUDY PLOTS
1954
BILLAPALOOLA PLANTATION
PLOT NO.1
PRE-1939
1 INCH=10 CHN APPROX.
1955
1956
PLOT NO.2
1957
1958
1958
1959
1963
PLOT NO.5
PLOT NO.3
1960
1961
1962
1961
PLOT NO.4
TO TUMUT
TO YASS
0 10 20 30
KILOMETERS (APPROX)
YASS
TUMUT
CANBERRA
A.C.T.
N.S.W.
KEY
ROADS
RIVERS
BOUNDARIES
CENTRAL RIDGE
SCALE
0 4 8 12 16
KILOMETERS (APPROX)

to 0.081 ha (0.20 ac). All plots were circular except plot 3 which was rectangular (40.2 x 20.1 m, 2 chn x 1 chn) and located obliquely to the line of tree rows to reduce the influence of boundary location on plot stocking. Details of the five study plots finally marked out in June 1966 are given in Table 2.1, Figs. 2.2 - 2.4 and Plates 2.1 - 2.3.

TABLE 2.1 P. radiata study plot details

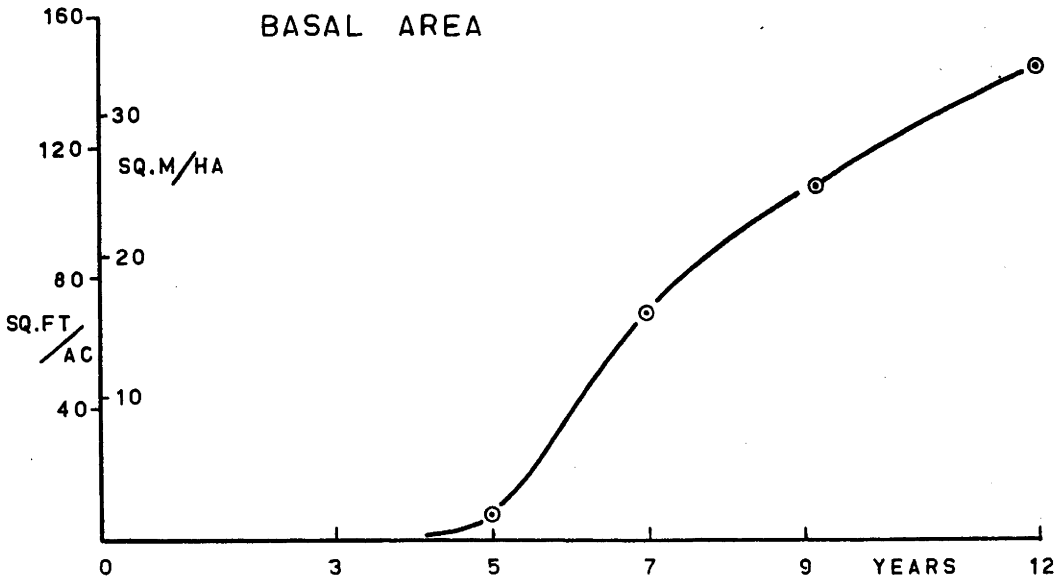
Plot number	1	2	3	4	5
Plantation compartment	69	143	182	228	238
Age in 1966 (years)	12	9	7	5	3
Plot area (hectares)	0.101	0.081	0.081	0.101	0.101
Stems per plot	158	119	118	151	150
Stems per hectare	1560	1470	1458	1492	1483
Mean D.B.H. (cm)	16.0	14.5	12.3	3.9	-
B.A. per ha (sq m)	32.8	25.0	16.0	2.0	-
Mean height (m)	15.6	12.1	7.9	3.1	1.4
Mean dominant height (m)	17.7	14.0	10.0	4.8	2.4

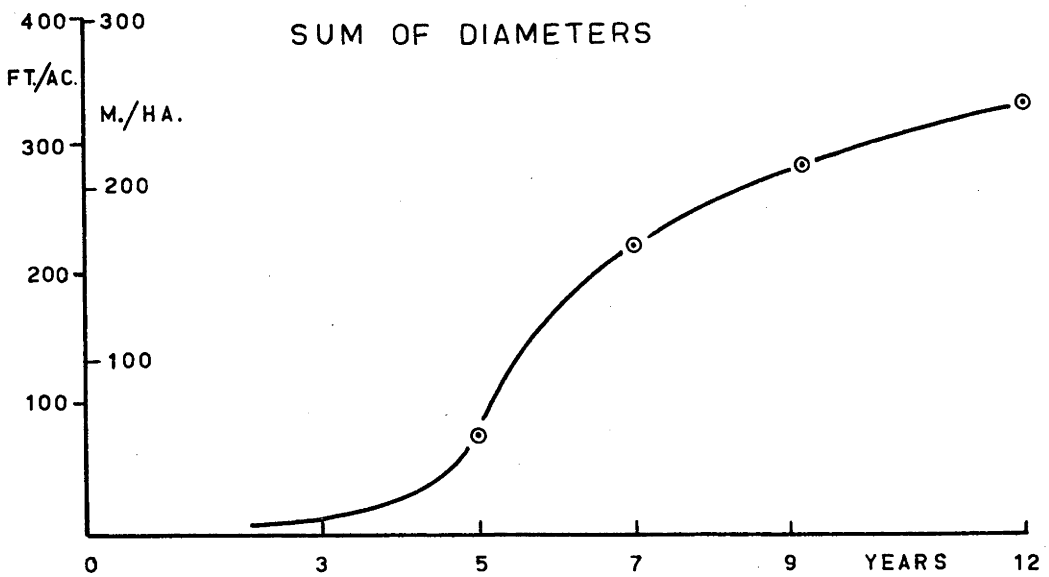
Over each plot stocking density was reasonably uniform. In plots 3 - 5, covering the period to canopy closure, stand weights were directly related to the number of trees present, and in these plots the numbers of trees per unit area are almost identical. For plot 1 (1560 stems/ha) complete canopy closure had occurred several years previously and the effect of slightly higher stocking density on stand weight and distribution was probably minimal (discussion of the significance of stocking density variations in Chapter 2.3.3 confirm this).

The study plots are on a site of better quality and are more heavily stocked than the average for the plantation as a whole (Fig. 2.3). The regular progression shown by diameter

FIG. 2-2 P.RADIATA STUDY PLOT DEVELOPMENT

BILLAPALOOLA PLANTATION





STUDY PLOT AGE

FIG. 2-3 P.RADIATA AGE—HEIGHT GROWTH

BILLAPALOOLA PLANTATION

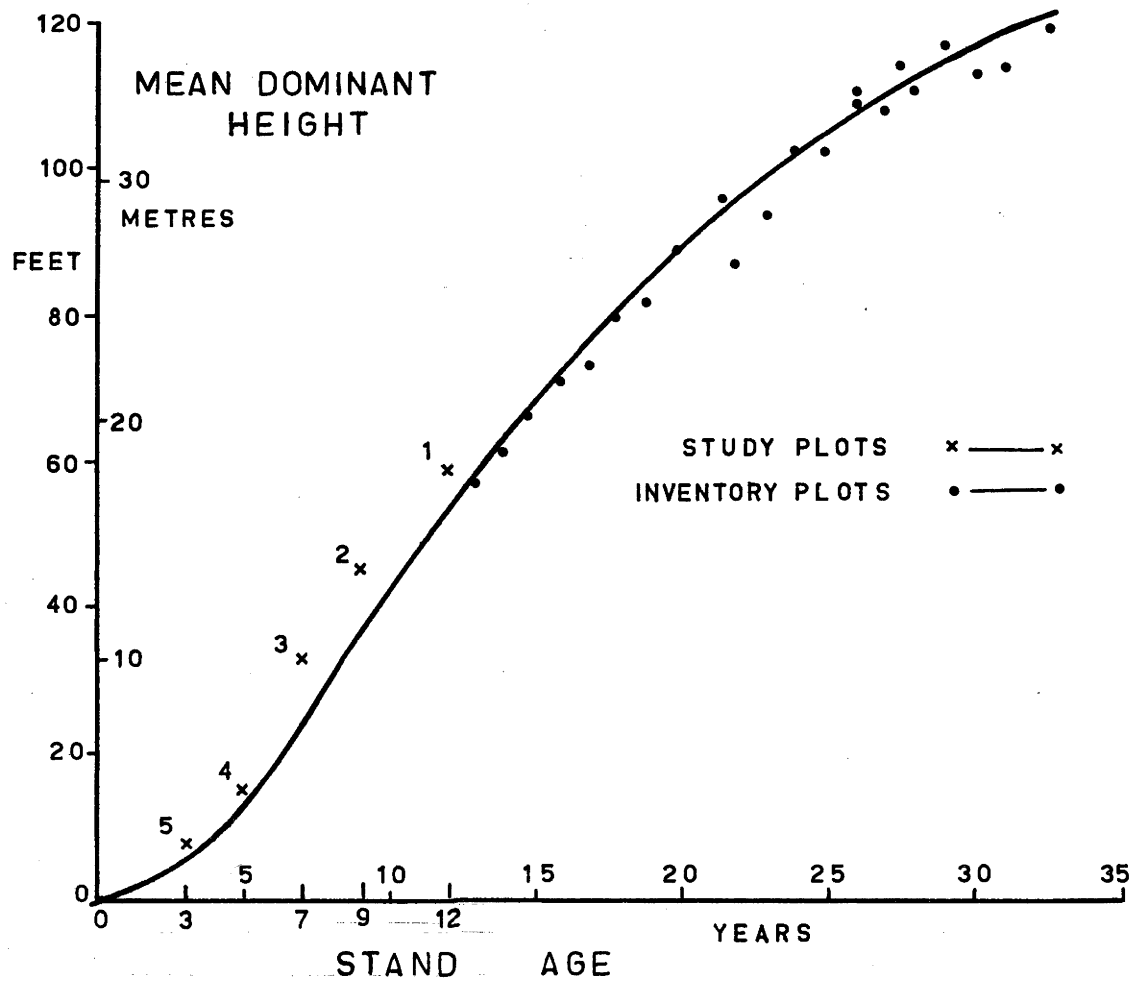


PLATE 2.1 a Billapaloola plantation. Plot 5 (3 years) of age series. Trees average 1.4 metres high. Note grass cover with bare patches.

PLATE 2.1 b Billapaloola plantation. Plot 4 (5 years) of age series. Trees average 3.1 metres high. Showing litter collection frame. Note increase in bracken fern and total ground cover.

PLATE 2.2 a Billapaloola plantation. Plot 3 (7 years) of age series. Trees average 7.9 metres high. Height growth rate increased since age 5. Lower branches on most trees touching.

PLATE 2.2 b Billapaloola plantation. Plot 2 (9 years) of age series. Trees average 12.1 metres high. All trees pruned of lower branches to 3 metres.

PLATE 2.3 a Billapaloola plantation. Plot 1 (12 years) of age series. Trees average 15.6 metres high.

PLATE 2.3 b Billapaloola plantation. Plot 1, showing litter collection frame.

distributions (Fig. 2.4), and the regular increase in all growth parameters (Figs. 2.2 and 2.3) indicate the plots can reasonably be assumed to form an age series on basically similar sites. Further confirmation of this might have been obtained by detailed annual growth records based on the measurement of heights of all previous winter resting nodes on the tree. This was not done since considerable variation in growth between years resulted from climatic variation, particularly in rainfall.

The amounts of organic matter contained in the understory vegetation and litter layers of a forest ecosystem vary considerably according to the interactions between many environmental and biotic factors. The understory vegetation may differ in both composition and amount with changes in tree stocking density (Baskerville, 1966) but rarely comprise much of the total biomass in a vigorous, closed tree community. The amount of litter present on the forest floor depends on the balance between annual litter fall and decomposition, both of which depend on climatic, edaphic and other environmental factors (Witkamp and van der Drift, 1961).

Within the study area both subordinate vegetation and litter layers vary considerably in content and type through the age sequence (Plates 2.1 - 2.3). The relative contribution of these components to the total biomass of the study plots, particularly in the youngest stands, is an important factor in any examination of organic dry matter distribution and nutrient balance.

2.2.3 History of the study plots

The history of the stands in which the study plots were located (Table 2.2) was obtained from reports made available by the N.S.W. Forestry Commission (unpublished, 1962). The species composition of the original vegetation was similar on each area. Pine seedlings for each annual planting were raised in one of three comparable nurseries nearby, from seed

TABLE 2.2 *P. radiata* stand history in study plot area

Study Plot	Year Planted	Original Vegetation	Seed Collection	Seedling Nursery	Regrowth Removed
1	1954	Over-mature eucalypts	probably Green Hills	Green Hills	1st 1954-55 2nd 1956
2	1957	E.dalrympleana E.viminalis E.radiata E.camphora	2nd thinnings Red Hill	Red Hill	1st 1958 2nd 1959 3rd 1962-3
3	1959	Over-mature E.dalrympleana E.viminalis E.radiata	2nd thinnings Red Hill	Red Hill	1st 1960 2nd 1961 3rd 1962-3
4	1961	Over-mature E.viminalis E.dalrympleana E.radiata E.dives	2nd thinnings Billapaloola	Billapaloola	1st 1962 2nd 1963
5	1963	Over-mature E.dalrympleana E.viminalis E.radiata E.dives	2nd thinnings Red Hill	Red Hill	1st 1964 2nd 1965

N.B. Green Hills, Red Hill and Billapaloola are similar high quality plantations in the Tumut region.

collected from trees felled in second thinning operations in local pre-1939 plantations.

Normally, woody regrowth from the original eucalypt forest is removed during the first few years after pine planting to prevent competition with the pines. All pine trees are low pruned when each plantation stand reaches eight years of age, all branches being removed to about 3 m height. Study plots 1 (1954) and 2 (1957) were pruned in 1962 and 1965 respectively. Whilst pruning influences nutrient distribution, this is part of the normal silvicultural operations for the forest.

2.2.4 Study plot environment

Only limited meteorological records are available (unpublished Forestry Commission report, 1962) for the plantation. The mean annual rainfall of the area is 145 cm (56.7 ins); with a lowest mean monthly rainfall of 7.6 cm (3.0 in) and summer minimum. The mean temperature of the coldest month is 4.2°C and of the hottest month is 19.0°C. Snow falls in most winters and may lie for two months; some snow damage was observed on trees in the plantation.

Soils of the area have been described generally by Northcote (1965, 1966). The soils at all plots are red earths derived in-situ from granite parent material, they are non-calcareous and show gradational change through the profile. The A horizons are sandy to sandy-loams, the B horizons are finer grained sandy-loams to loams. Granite boulders in various stages of degredation can be found on the surface and through the profile. The profiles are at least 75 cm (30 in) deep to decomposing granite country rock.

Soils samples of the A 0 - 10 cm and B 20 - 30 cm horizons were collected at five locations (plot centre and four corners) in each study plot. Following hydrogen flouride extraction, the samples were analysed for total nutrients (Table 2.3). All nutrient elements determined

TABLE 2.3 Nutrient status of the P. radiata study plot soil (means of five soil samples per study plot)

		Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Phosphorus (% dry weight)						
A	0 - 10 cm	0.18	0.11	0.15	0.19	0.14
B	20 - 30 cm	0.12	0.15	0.15	0.12	0.11
Calcium (% dry weight)						
A	0 - 10 cm	0.24	0.20	0.25	0.24	0.21
B	20 - 30 cm	0.28	0.26	0.22	0.18	0.18
Potassium (% dry weight)						
A	0 - 10 cm	0.63	0.77	1.10	0.51	0.23
B	20 - 30 cm	0.67	0.89	1.03	0.35	0.24
Magnesium (% dry weight)						
A	0 - 10 cm	0.19	0.16	0.13	0.19	0.23
B	20 - 30 cm	0.19	0.17	0.10	0.25	0.29
Manganese (ppm)						
A	0 - 10 cm	550	520	430	670	630
B	20 - 30 cm	390	250	420	370	420
Zinc (ppm)						
A	0 - 10 cm	30	20	14	38	29
B	20 - 30 cm	32	31	25	38	31

occur relatively abundantly in all plots and this is typical of the soil type (F.R. Humphreys, pers. comm.). There is no evidence of nutrient deficiency in the area, and the variation in the nutrient content of the soils at each plot is insufficient to influence growth and is not reflected in the nutrient content of the trees (Chapter 5.3.3).

2.2.5 Field sampling and laboratory procedures

(a) The P. radiata trees

Tree sampling began before the results given in Chapter 1 were available, but these results support the validity of the methods used in the estimation of dry weight.

The height and bole diameter at breast height (D.B.H.O.B.) of all trees in the plots were measured just prior to sampling. The bole diameter range for the trees of each plot was divided into five classes of progressively larger diameter with equal numbers of trees in each class. Two trees were randomly selected from each class for weighing and chemical analysis. Harvesting of sample trees commenced in June 1966. Either one or two trees were taken from each plot at roughly weekly intervals until by mid-August nine trees per plot had been collected (a total of 45 trees). Heavy rain and snow delayed the collection of the 10th tree for several weeks, by which time substantial growth had taken place; consequently the 10th tree was not included in the sample.

Each tree was cut at ground level, then all previous winter resting nodes were identified as far down the tree as possible (fully for trees in plots 3, 4 and 5, and at least the five previous years for trees of plots 1 and 2). The bole was cut at each winter node to give successive vertical annual growth zones (or age-strata). For each age strata of each tree the major components were grouped as separate units.

Only the uppermost 1965-66 age strata contains material of a single years growth. Successively lower age-strata

include material of an increasing age range; for example, the 1964-65 age-strata contains 1- and 2-year old material in each component and the 1963-64 age-strata contains 1-, 2- and 3-year old material. Leaves growing along the bole are of only one years growth in each age-strata. A preliminary study of a five year old stand in the same area had indicated that many more trees than could be handled would be required before the results of more intensive subdivision would be reliable because of the increasing variation between trees with increasing subdivision.

Female cones were found on trees in plots 1, 2 and 3 only. The cones on each sample tree were not subdivided into age-strata but were grouped into a single sample for each tree. Male cones mature in late spring and were not present at the time of sampling, but later in the year male cone parts were collected as litter (Chapter 3.3). Only above ground parts were sampled in this study but an estimate of root producation has been made from reference to other studies.

Sample trees were collected, one or two from each plot, at weekly intervals so all material from each collection could be dried quickly and sufficiently within the week to prevent respiration losses. All sample material was eventually dried to constant weight at 85^{o}C.

When the oven dry weights of the boles had been recorded each age-strata was sampled by removing full width discs 2 - 4 cm thick at 0.5 - 1 metre intervals along the bole. The bark was removed from each disc and its weight as a proportion of the total disc weight recorded, so total weights of bole bark and bole wood could be calculated separately.

The number of units into which each tree was subdivided increased with tree age, tree size and the confidence with which the age-strata could be identified. Each tree of plot 1 (12 years old) was divided into as many as 35 component/ age-strata units.

2.2.5 (b) The understory vegetation and litter layers

As the pine stands develop through the age series, the amount of subordinate vegetation (which increasingly becomes an understory as the pine trees mature) decreases and the amount of litter on the forest floor increases. Some intermixing of the two components was evident, for example, pine needles were found lying on top of, within and underneath grass tussocks. Consequently, both the subordinate vegetation and the litter layers were sampled together. Large growing woody species had been manually cleaned from all study plots in routine management operations (Table 2.2) so members of the subordinate vegetation were small, being mainly native grasses (particularly Poa spp.) and bracken fern (Pteridium aquilinum).

Immediately before the sample trees were felled twenty quadrats, each 1/16 sq. metres, were located randomly in each sample plot. The ground vegetation within each quadrat was carefully clipped at ground level and was subdivided into species groups. The litter layer was then carefully collected from within the quadrat frame and subdivided into two categories, undecomposed (L-layer) and decomposing (F and H layers). All material from each quadrat was oven dried at 85°C prior to weighing.

2.3 RESULTS - DRY WEIGHT OF THE STAND COMPONENTS

2.3.1 Dry weights of the sample trees

The bole diameters and heights of the nine sample trees from each of the five study plots are listed in Table 2.4 a - e. The diameters of the sample trees give a reasonable representation of each population (Fig. 2.4). The sample trees tend to be concentrated through the central diameter classes because selection was made from classes of equal numbers of trees.

FIG. 2·4 P.RADIATA SIZE CLASS FREQUENCY DISTRIBUTIONS

BOLE DIAMETER PLOTS 1–4. BOLE HEIGHT PLOT 5.

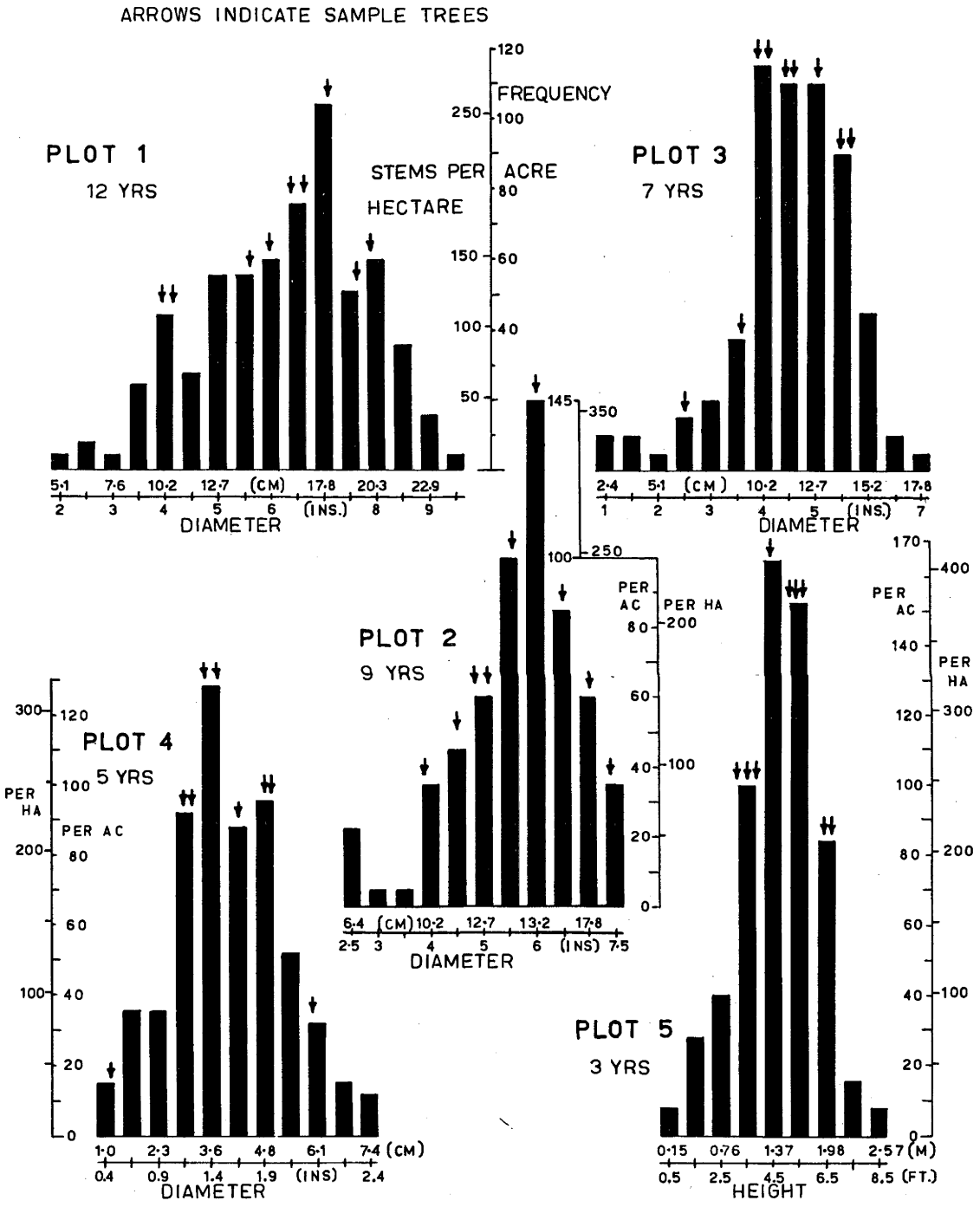


TABLE 2.4a P. radiata age series Sample tree size and dry weight values

	Plot 1 Age 12 years								
Tree number	1	2	3	4	5	6	7	8	9
Bole D.B.H. (cm)	10.3	10.4	14.5	15.3	16.1	16.3	18.0	19.8	19.8
Height (m)	13.3	13.7	15.2	16.2	16.0	15.8	16.2	15.8	17.8
B.A. x Ht. (cu m)	0.11	0.12	0.25	0.30	0.33	0.33	0.41	0.49	0.55
Dry weights (kg)									
Branch wood	2.73	2.32	6.16	11.34	8.34	13.85	12.84	20.66	24.84
Branch leaves	1.05	1.02	2.87	4.79	5.43	5.18	8.88	10.31	9.86
Bole leaves	0.07	0.48	0.18	0.17	0.18	0.25	0.19	0.42	0.21
Bole bark	2.98	2.87	7.03	3.95	4.94	5.81	6.10	7.21	10.22
Bole wood	18.90	18.29	37.78	49.88	47.08	50.85	66.79	74.87	86.64
Cones	0.37	-	0.65	0.09	0.10	1.72	1.97	-	-
Total tree	29.09	24.97	54.65	70.22	66.08	77.66	96.77	113.48	131.76

TABLE 2.4b *P. radiata* age series Sample tree size and dry weight values

	Plot 2 Age 9 years								
Tree number	1	2	3	4	5	6	7	8	9
Bole D.B.H. (cm)	9.7	11.6	12.1	13.1	14.3	17.6	15.4	16.6	18.4
Height (m)	9.8	10.8	11.9	11.0	13.8	12.1	12.0	12.2	13.7
B.A. x Ht. (cu m)	0.07	0.11	0.14	0.15	0.22	0.29	0.23	0.27	0.36
Dry weights (kg)									
Branch wood	2.90	4.19	5.46	4.76	6.10	6.72	7.41	9.33	13.22
Branch leaves	2.97	4.69	5.44	4.17	5.52	5.13	7.18	7.43	8.44
Bole leaves	0.30	0.47	0.18	0.13	0.25	0.12	0.31	0.27	0.25
Bole bark	1.89	1.99	2.61	3.83	4.63	3.76	4.26	4.78	5.82
Bole wood	13.29	17.55	25.50	26.89	36.57	38.62	33.21	39.47	57.16
Cones	-	-	2.30	0.30	-	1.82	-	0.01	-
Total tree	21.34	28.89	41.49	40.08	53.06	56.16	52.37	61.29	84.89

TABLE 2.4c P. radiata age series Sample tree size and dry weight values

	Plot 3 Age 7 years								
Tree number	1	2	3	4	5	6	7	8	9
Bole D.B.H. (cm)	6.4	9.6	9.6	10.6	10.9	11.3	13.1	13.6	14.5
Height (m)	6.1	8.4	6.7	8.7	7.7	8.5	9.1	9.1	8.1
B.A. x Ht. (cu m)	0.002	0.060	0.048	0.076	0.071	0.085	0.122	0.133	0.134
Dry weights (kg)									
Branch wood	1.03	3.43	6.72	6.18	6.27	7.18	13.23	17.35	22.18
Branch leaves	1.41	4.70	4.93	5.22	6.17	7.75	11.46	12.42	9.23
Bole leaves	0.24	0.39	0.20	0.32	0.35	0.44	0.36	0.30	0.24
Bole bark	0.67	1.05	1.11	1.46	1.22	1.65	2.57	3.22	3.21
Bole wood	3.53	9.78	7.99	11.20	12.49	13.36	18.14	23.25	20.71
Cones	-	-	-	-	-	0.05	0.36	0.38	0.28
Total tree	6.88	19.35	20.94	24.37	26.50	30.43	46.13	56.93	55.85

TABLE 2.4d. P. radiata age series Sample tree size and dry weight values

	Plot 4 Age 5 years								
Tree number	1	2	3	4	5	6	7	8	9
Bole D.B.H. (cm)	1.4	2.8	3.2	3.5	3.9	4.1	4.8	5.1	5.8
Height (m)	2.1	2.6	2.6	3.0	2.7	3.4	3.4	3.8	3.7
B.A. x Ht. (cu m x 10^{-3})	0.03	0.2	0.2	0.3	0.3	0.5	0.6	0.8	1.0
Dry weights (kg)									
Branch wood	0.04	0.34	0.41	0.83	0.51	0.56	0.91	0.90	2.10
Branch leaves	0.13	0.70	0.90	1.18	0.90	1.21	1.17	1.87	2.64
Bole leaves	0.09	0.08	0.13	0.09	0.16	0.11	0.15	0.23	0.16
Bole bark	0.05	0.10	0.16	0.19	0.14	0.21	0.24	0.31	0.36
Bole wood	0.26	0.65	1.06	1.14	1.10	1.37	1.77	1.88	2.62
Total tree	0.57	1.86	2.66	3.44	2.80	3.45	4.24	5.18	7.87

TABLE 2.4e *P. radiata* age series Sample tree size and dry weight values

	Plot 5 Age 3 years								
Tree number	1	2	3	4	5	6	7	8	9
Bole height (m)	1.0	1.1	1.2	1.4	1.6	1.6	1.8	2.0	2.1
Dry weights (kg)									
Branch wood	0.030	0.025	0.084	0.115	0.130	0.150	0.227	0.167	0.158
Branch leaves	0.074	0.086	0.230	0.283	0.348	0.352	0.450	0.443	0.555
Bole leaves	0.026	0.037	0.040	0.062	0.040	0.084	0.084	0.100	0.107
Bole bark	0.012	0.022	0.045	0.047	0.059	0.059	0.064	0.058	0.077
Bole wood	0.039	0.076	0.197	0.248	0.254	0.268	0.282	0.261	0.338
Total tree	0.181	0.246	0.597	0.755	0.831	0.914	1.110	1.030	1.235

Component dry weight values (Table 2.4) are the summed weights for the several age-strata of each component. Subsequent calculations are based on component and total tree dry weights because age-strata weights vary greatly between trees (Table 2.5), but individual age-strata samples were retained for chemical analysis. The weight of components in each age-strata was not closely related to tree size, but probably more closely to variation between trees in their previous growth flushes; for example, sample trees 5 and 6 of plot 1 (Table 2.5) are of comparable size and the total weights of leaves are similar, but the distributions of leaf weights differ markedly through their upper crowns.

TABLE 2.5 Distribution of leaf weight through the upper crown of sample trees P. radiata age series

Sample Tree	B.A. x Height (cu m)	Plot 1 Age 12 years Leaf dry weight (kg) Age-Strata 1965-66	1964-65	1963-64	1962-63
1	0.10	0.03	0.39	0.40	0.07
2	0.12	0.15	0.25	0.42	0.07
3	0.25	0.32	0.85	1.05	0.56
4	0.30	0.52	1.62	0.94	1.02
5	0.33	0.43	0.65	1.38	1.95
6	0.34	0.35	1.23	1.16	0.82
7	0.41	0.10	1.52	1.17	1.95
8	0.49	0.68	0.99	3.01	1.27
9	0.55	0.37	1.42	2.45	2.12
Mean		0.33	0.99	1.33	1.09

Sample trees varied greatly in size both within and between plots. The total dry weight of the largest sample tree per plot was 131.7, 84.9, 56.9, 7.9 and 1.2 kg for plots 1 to 5 respectively, and these trees were 5.3 x, 4.0 x, 8.3 x, 13.9 x and 6.8 x the total weights of the smallest tree sampled from those plots. The range of sample tree weights is much less than the total range for each plot.

Cones were found on six of the nine sample trees in plot 1 and four trees in both plots 2 and 3. Tree 3 of plot 2 had the greatest weight of cones, 2.3 kg, but the average weight of cones per tree was greatest for plot 1.

No sample tree had many dead branches because trees in the oldest plots (1 and 2) had been pruned and the lowest branches remaining after pruning usually held some green leaves. Consequently branch wood and branch leaves were each treated as single components, stratified into age-strata. Experience of the 100-tree population (Chapter 1) has shown the difficulty in reliably estimating the weight of dead branches per unit area within young stands.

2.3.2 Sample plot dry weights

(a) Calculation of regression equations

Numerous relationships between sample tree weights and linear dimensions were examined for each study plot. Both direct multivariate and transformed variable relationships were examined (Table 2.6). Inevitably with so many regression equations for relatively small samples some inconsistencies arise by chance. However, the relative significance of the several equations calculated for study plots 1 to 4 is very similar to the relative significance of similar equations calculated for the 100-tree population (c.f. Tables 1.6 and 1.7).

Equations of the form:

$$\text{Log}_e \text{ weight} = a + b \log_e (\text{B.A.} \times \text{Ht.}) \qquad \text{Equation 1}$$

show the greatest significance most consistently, and this is in accordance with the theoretical implications discussed in Chapter 1. Consequently equations of this form have been adopted for all subsequent dry weight calculations, even though in some situations other equations appear more significant.

TABLE 2.6 Significance of sample tree regressions - P. radiata age series T - values for regressions of component and total tree dry weight on several size variables $T = b/S.E._b$ For significance ($P = 0.01$), $T = 3.50$

Independent variable (Bole size)	Plot 1 Branch Wood	Branch Leaves	Bole Bark	Bole Wood	Total Tree	Plot 2 Total Tree	Plot 3 Total Tree	Plot 4 Total Tree
Direct	Weight = a + b x							
Diameter	6.30	9.57	3.92	12.28	11.25	6.66	10.05	7.10
Basal area	7.56	13.07	4.10	15.91	15.33	6.68	14.87	9.88
Diam. x Ht.	7.17	7.93	4.33	16.20	13.97	11.28	7.23	8.18
B.A. x Ht.	8.93	10.81	4.53	26.38	24.83	10.05	14.29	9.61
Log.: log.	Log_e weight = a + $bLog_e$ x							
Diameter) Basal area)	11.27	17.10	4.86	22.66	23.24	8.24	28.73	14.17
Diam. x Ht.	11.70	14.45	4.83	26.24	23.94	14.33	10.41	13.23
B.A. x Ht.	11.83	16.19	4.87	27.95	26.65	11.98	15.84	14.23

Bole diameter was not measured in plot 5 because the trees were small, averaging only 1.4 m (4.7 ft) high. There is a curvilinear relationship between height and weight for the sample trees in this plot (Fig. 2.7), weight being significantly related to Log_e height.

Consequently equations of the form:

$$\text{weight} = a + b \, Log_e \text{ height} \qquad \text{Equation 2}$$

were calculated for each of the major components and used for the calculation of stand weight in plot 5.

All equations used in the calculation of stand component and total dry weight were significant for all plots at $P = 0.01$ level; except for stem leaves, where the equations were:

not significant for plots 1 and 2
significant at $P = 0.1$ for plot 3
significant at $P = 0.05$ for plot 4
significant at $P = 0.01$ for plot 5

and for female cone weights in plots 1 and 2. However, the weights of cones and stem leaves are only a small proportion of total tree weights, and separate accurate estimates of their weights are not required.

(b) Comparison of regression equations

The regression equations for each component can be compared both between study plots (Table 2.7) and with comparable equations reported for other studies (Table 2.8). The trees in plot 4 (5 years old) are small and have not developed a normal tree habit, so it is not surprising the equations calculated for this age class differ from those calculated for older trees, particularly for trees in closed stands.

Allometric regression of bole weight on bole diameter suggests that the sample trees of plot 2 are anomalous (Table 2.7)

TABLE 2.7 Values for regression coefficient "b" in Log_e weight = a + b Log_e bole size for *P. radiata* in age series and 100-tree plot

P. radiata stand	Age Series				100-tree plot
	Plot 1	Plot 2	Plot 3	Plot 4	
Stand age (yrs.)	12	9	7	5	8
Leaves					
D.B.H.	3.32	1.15	2.42	1.69	2.66
D.B.H. x Ht.	2.44	0.84	1.61	1.16	1.55
B.A. x Ht.	1.41	0.49	0.99	0.69	1.01
Branch wood					
D.B.H.	3.32	1.99	3.67	2.50	2.91
D.B.H. x Ht.	2.46	1.41	2.31	1.70	1.62
B.A. x Ht.	1.42	0.84	1.44	1.02	1.07
Bole					
D.B.H.	2.27	1.99	2.32	1.59	2.43
D.B.H. x Ht.	1.68	1.43	1.55	1.09	1.46
B.A. x Ht.	0.97	0.84	0.94	0.65	0.94
Total tree					
D.B.H.	2.42	1.85	2.66	1.74	2.55
D.B.H. x Ht.	1.79	1.34	1.74	1.19	1.48
B.A. x Ht.	1.03	0.79	1.07	0.71	0.97

TABLE 2.8 Typical values reported for the regression coefficient "b" in the equation - Log dry weight = a + b Log bole diameter for forest stands

Species		Component			
		Leaves	Branches	Bole wood	Total tree
White birch	(1)	2.94	3.30	2.36	2.48
White spruce	(1)	2.85	2.78	2.36	2.48
Balsam fir	(1)	3.21	3.22	2.28	2.53
Short-leaf pine	(2)	1.73	2.57		
Sitka spruce	(3)				2.43
Scots pine	(3)				2.41
Scots pine	(4)				2.5
Scots pine	(5)	3.60	3.53	2.23	2.47
Douglas fir	(6)	1.96			
Red pine	(6)	2.56			
Jack pine	(6)	2.87			
White pine	(6)	2.09			
Loblolly pine	(7)	2.67			
Betula spp.	(8)				2.60
Eucalyptus obliqua	(9)	2.65	3.48		
Radiata pine present study					
Plot 1 age 12 yrs		3.32	3.32	2.27	2.41
Plot 2 age 9 yrs		1.15	1.99	1.99	1.85
Plot 3 age 7 yrs		2.42	3.67	2.32	2.66
Plot 4 age 5 yrs		1.69	2.50	1.59	1.74
100-tree plot, age 8 yrs		2.66	2.91	2.43	2.55

References

(1) Baskerville, 1965a.
(2) Loomis, et al., 1966.
(3) Rutter, 1955.
(4) Ovington, 1957.
(5) Ovington and Madgwick, 1959b.
(6) Kittredge, 1944.
(7) Rogerson, 1964.
(8) Ovington and Madgwick, 1959a.
(9) Attiwill, 1966a.

as the regression coefficient, b, for this plot is 1.99 while that for the older and younger plots and the 100-tree plot (Chapter 1) range from 2.27 to 2.43. However, regressions of bole weight on (D.B.H. x Ht) and on (B.A. x Ht) are similar for all plots, which indicates the apparent anomaly is due to variable bole form within plot 2. Because both (B.A. x Ht) and bole weight are related directly to bole volume, the regression coefficient for allometric regressions of bole weight on (B.A. x Ht) would normally approximate to 1. The value may differ from 1 when the overbark measurement of diameter does not reflect a constant proportion of underbark wood volume through the range of size classes, which possibly is the case for plot 4 or when the tree form varies substantially through the range of size classes, as might be expected in plot 2 where through increasing competition individual tree diameter growth is restricted (Fig. 2.2) but height growth, particularly of the dominants, is still at a maximum (Fig. 2.3).

The regressions of $\log_e$ bole weight on $\log_e$ (B.A. x Ht) used to calculate stand bole weights are very nearly identical through the range of values common to the older plots 1 - 3 (Fig. 2.5).

The coefficient for regressions of $\log_e$ leaf weight on $\log_e$ bole diameter changes from 1.7 for the immature trees of plot 4 to 3.3 for the oldest trees where closed canopy conditions have been established (Fig. 2.8). This progression includes the eight year old stand of 100-trees (Chapter 1). Similar progressions with tree age in the allometric relationship between leaf weight and bole size has been demonstrated for a number of species (Tadaki, 1966).

This progressive increase in the regression coefficient expresses differences in relative rates of development between dominated and dominant trees. Before canopy closure the crowns of all trees enlarge although the overall rate of increase varies between stands. Once a continuous canopy cover has

FIG. 2-5 BOLE WEIGHT x VOLUME RELATIONSHIPS IN P.RADIATA AGE SERIES

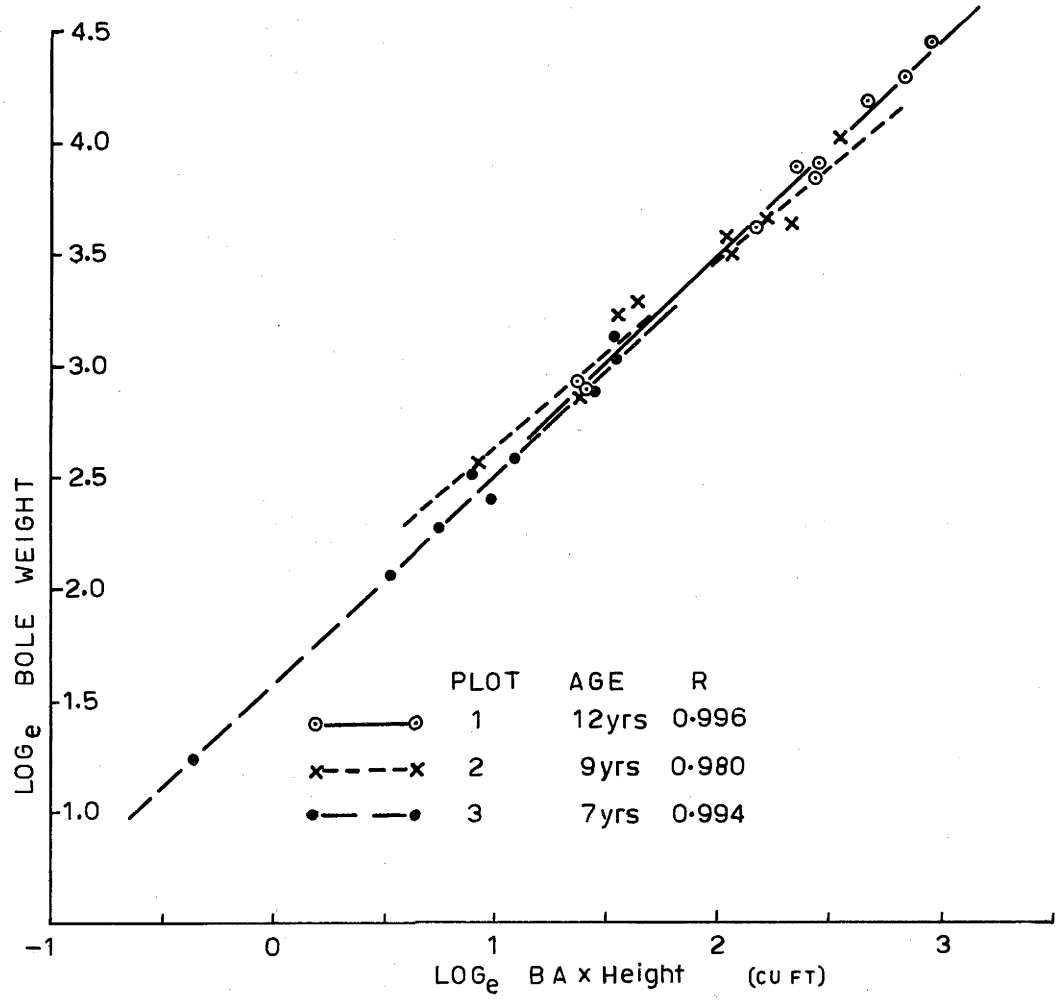


FIG. 2-6 TOTAL DRY WEIGHT x BOLE VOLUME RELATIONSHIPS FOR PLOTS 1–4 OF P. RADIATA AGE SERIES

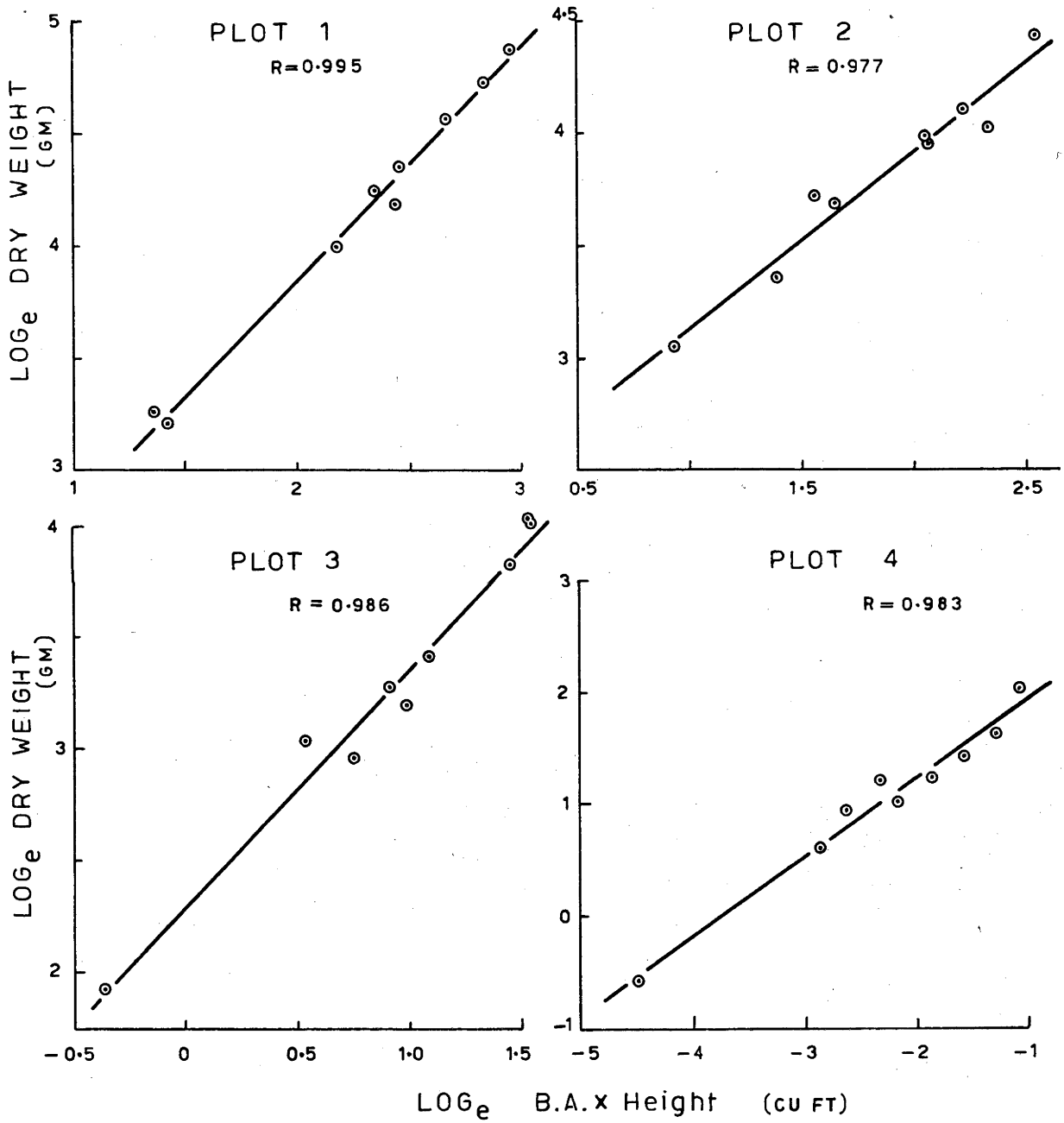


FIG.2-7 TOTAL DRY WEIGHT x BOLE HEIGHT RELATIONSHIPS IN P. RADIATA STUDY PLOT 5

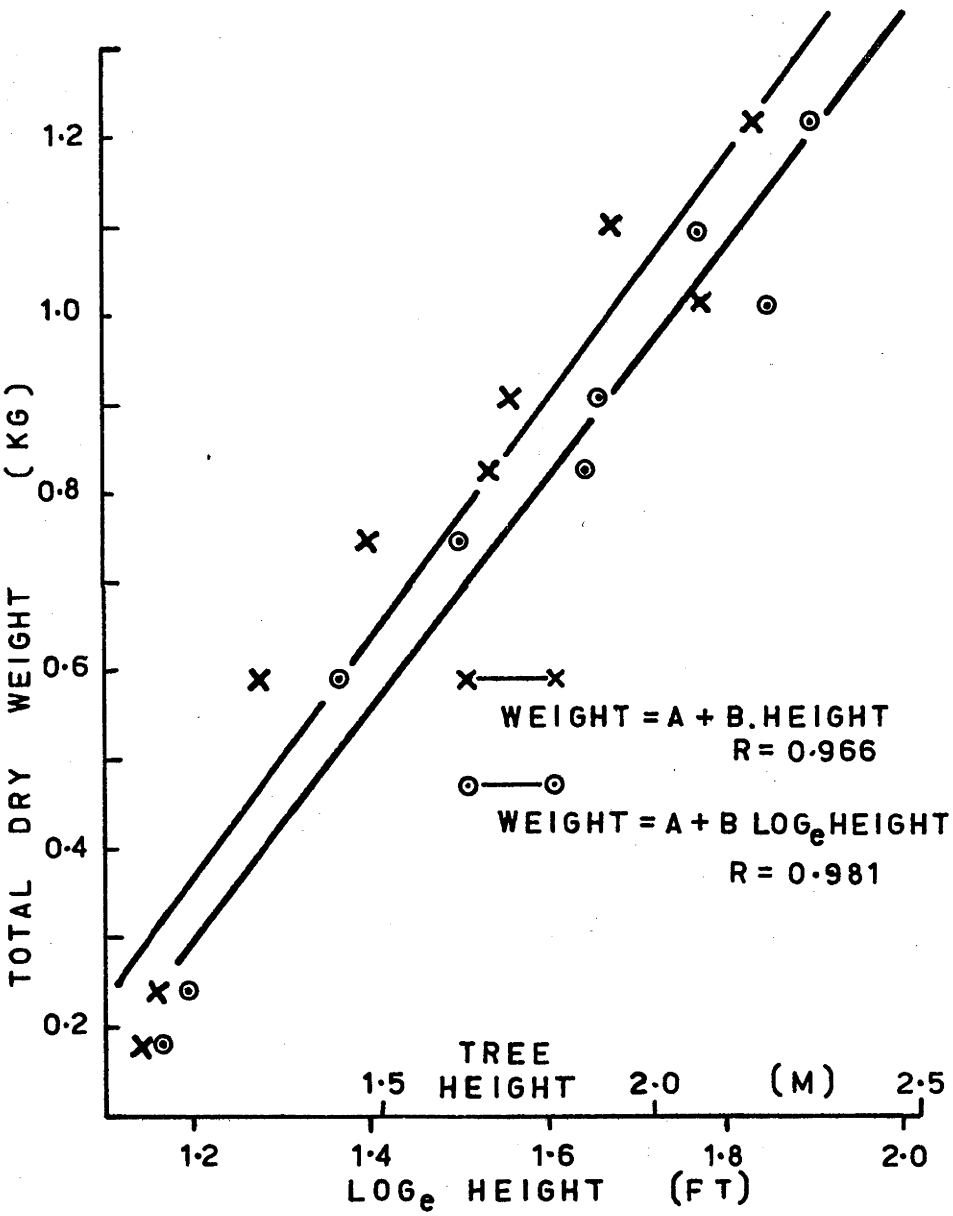
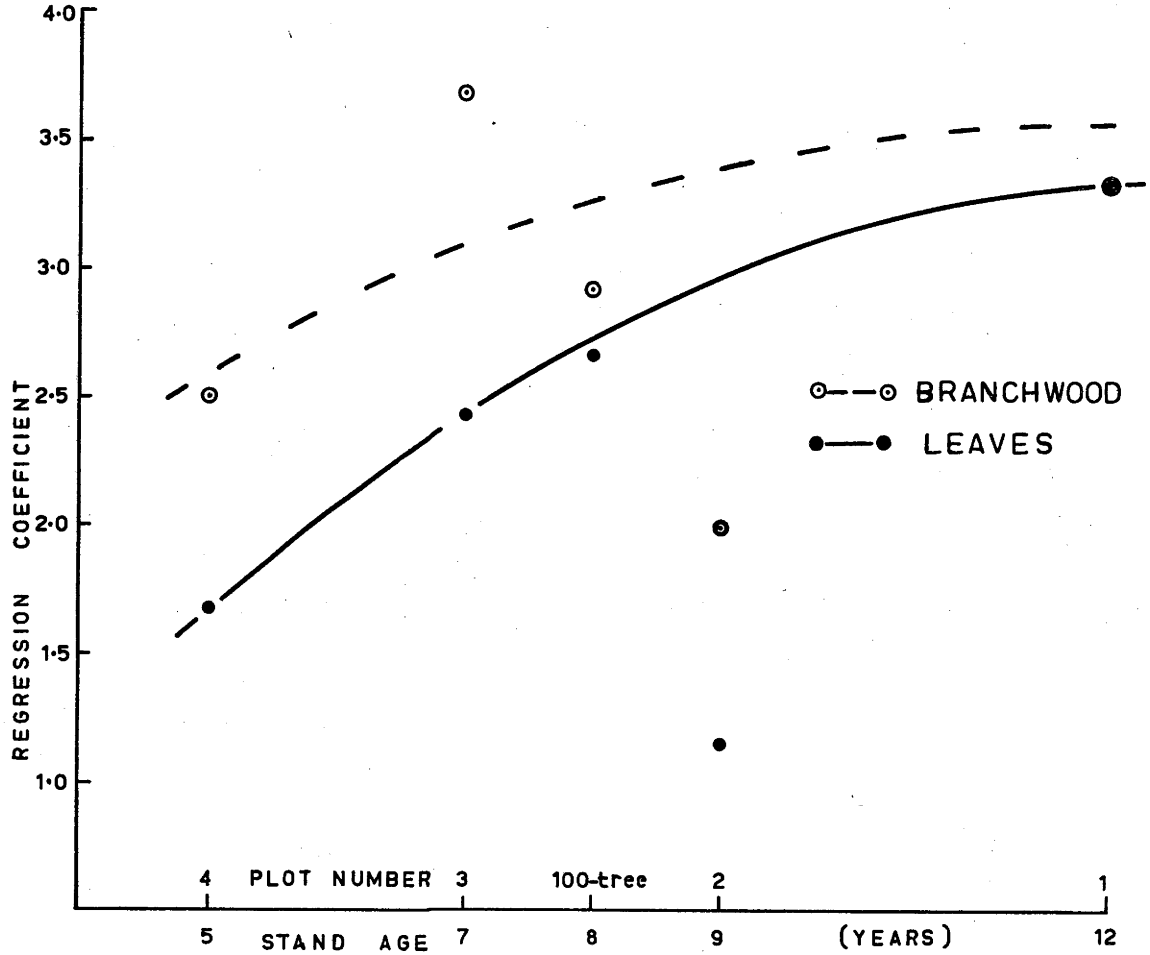


FIG. 2-8 VALUES FOR REGRESSION COEFFICIENT IN EQUATION Log_e weight = a + b Log_e d.b.h. FOR P.RADIATA STANDS



developed the rate of increase of the crowns of dominated trees becomes progressively less than for dominant trees and the crowns of supressed trees may even decrease while their boles continue to grow slowly. Consequently the weight of leaves in a tree 10 cm diameter and 8 m high at 7 years is about 7 kg (e.g. codominant trees in plot 3) and by 12 years the tree may be 15 cm diameter and 15 m high and have the same weight of foliage (e.g. codominant trees in plot 1).

The divergence in relative development of dominant and dominated trees within an even-aged forest is restricted by physiological limitations on the dominants and the eventual death of supressed trees. No deaths from supression were evident in the study plots but for several of the smallest trees death appeared imminent. In a similar stand in New Zealand of slightly better site quality described by Spurr (1962), 40 of the original 1525 trees per hectare died by age 12 years but a further 360 trees per hectare died in the following 6 years. The maximum value for the regression coefficient cannot be predicted from the present data, but if the maximum coincides with death through supression of the smallest trees, as is likely, then the value for plot 1 (i.e. 3.32) is probably close to the maximum.

The similar increase in regression coefficient with increasing spacing shown by Tadaki (1966) for Cryptomeria seedings probably reflects the greater relative development of larger seedlings which is possible at wider spacings before competition is established.

The value of "b" (leaf dry weight x diameter) in plot 2 has been artifically reduced by the removal of a substantial weight of leaves from a constant length (3 m = 10 ft) along the lower bole by pruning at age 8 years. The value in plot 1 has not been influenced markedly by pruning since most of the branches removed in pruning would have been dead and devoid of leaves by age 12 years. The lowest branches remaining at 12 years carried only a minimum of green leaves and few shoots or leaves were being produced.

Attiwill (1966a) compared values for comparable regression equations for leaf and branch wood weights of Eucalyptus obliqua with a range of regression coefficient values for other species. The range of regression slopes ("b" values) for the plots in this study is as great as the range shown for widely contrasting species (Table 2.8). Chuong (1967) showed for P. radiata the slope of leaf weight regression equations may vary between contrasting sites. In the present investigations, site variation is considerable between the two study areas, for example dominant height of the 100-tree plot at age 8 years = 10 m (32.6 ft), for the age series plot 2 at 9 years and plot 3 at 7 years the dominant heights = 14 m (45.8 ft) and 10 m (32.9 ft) respectively, but this has had much less effect on the regression equation than either stand age or the artificial effect of pruning.

Small "b" values may also result in stands where nutrient deficiency, drought or disease may have lead to premature shedding of older leaves. The unusually small value (1.73) reported for P. echinata (Loomis, et al., 1966) may have resulted from such factors or may be a natural feature of short-leaf pine. Allometric relationships for branch wood weight on bole size show a similar progression for regression coefficients with age (Fig. 2.8), except that:

(i) the regression coefficient for plot 1 is a true value for live branch weight but is smaller than a true value for total branch weight, since without pruning most of the branches removed by pruning would be present but dead at age 12 years.

(ii) the 100-tree plot does not fit the trend established by the other plots due to the lower rate of branch wood growth in that plot (Chapter 1).

Attiwill (1966a) suggests the value of "b" in the total shoot - diameter relationship in non-senile stands must be greater than 2.0 because bole wood weights for individual

trees must be closely related to $(\text{d.b.h.o.b.})^{2.0}$ and canopy weights were shown to be closely related to $(\text{d.b.h.o.b.})^{3.0}$. In fact, because bole wood weights are directly related to both diameter and height, and height tends also to increase but less than diameter so bole wood weights are usually related to $(\text{diameter})^{>2.0}$ (i.e. in the allometric equation the regression coefficient >2). The regression coefficient in the total weight-diameter relationship may be less than 2 in very young stands, in recently pruned stands, in stands where some external factor such as drought or nutrient deficiency has disturbed the normal balance and possibly also in stands recently thinned by the removal of the dominated trees. Consequently for the very young plot 4 and for the pruned plot 2 the regression coefficient is less than 2.0. Total tree dry weight on bole basal area x height relationships for plots 1 - 4 are shown in Fig. 2.6.

(c) Calculation of stand dry weights

Component and total tree dry weights per plot were calculated by solving Equation 1 (plots 1 - 4) and Equation 2 (plot 5) for all trees in each plot, using appropriate pairs of regression constants and coefficients (Table 2.9) for each component or total tree. Some small variation exists in the values for total stand dry weight calculated by summing the stand weights for the several components or by solving the total tree regressions (Table 2.10); values calculated by the latter method are preferred in discussions of stand total dry weights.

Confidence limits appropriate to each major component and total tree weight estimate were calculated from the equations:-

$$\text{Variance} = \delta^2(1/n + \Sigma(X - \bar{x})^2 / [x^2])$$

where δ^2 = residual sums of squares of regression

n = number in sample

$X - \bar{x}$ = difference between population values of x and the sample mean

$[x^2]$ = corrected sums of squares of x.

TABLE 2.9 Regression constants used for the calculation of component and total tree dry weights in study plots

Plots 1 - 4 Log_e weight = a + b Log_e(B.A. x Ht)

Plot 5 Weight = a + b Log_e Height

Component	Branch Wood	Branch Leaves	Bole Leaves	Bole Bark	Bole Wood	Cones	Total Tree
Plot 1							
a	5.824	4.783	4.736	7.065	8.471	4.851	8.701
b	1.419	1.543	0.263	0.653	0.969	0.547	1.029
$S.E._b$	0.124	0.087	0.385	0.141	0.035	1.490	0.038
Plot 2							
a	7.207	7.601	5.872	6.848	8.714	10.515	9.265
b	0.808	0.533	-0.222	0.702	0.845	-2.455	0.781
$S.E._b$	0.120	0.129	0.323	0.129	0.070	2.385	0.070
Plot 3							
a	7.476	7.715	5.572	6.569	8.492	-0.742	9.203
b	1.437	1.049	0.156	0.840	0.937	4.296	1.065
$S.E._b$	0.190	0.095	0.156	0.050	0.042	0.500	0.068
Plot 4							
a	8.498	8.632	5.367	6.415	8.459		9.561
b	1.015	0.798	0.238	0.574	0.645		0.706
$S.E._b$	0.111	0.072	0.089	0.058	0.043		0.054
Plot 5							
a	-0.221	-0.602	-0.090	-0.062	-0.303		-1.277
b	0.218	0.586	0.099	0.071	0.334		1.307
$S.E._b$	0.036	0.041	0.018	0.008	0.036		0.092

TABLE 2.10 *P. radiata* age series. Stand dry weights (Kg x 10^3 per ha) and component weights as percent of total dry weights

Component	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
	12 years	9 years	7 years	5 years	3 years
Branch wood	18.73	9.91	14.92	1.20	0.166
%	15.8	13.5	29.4	21.5	15.6
Branch leaves	9.24	8.38	11.22	1.90	0.435
%	7.8	11.4	22.1	34.1	41.1
Bole leaves	0.33	0.35	0.44	0.19	0.086
%	0.3	0.5	0.9	3.5	8.2
Bole bark	8.81	5.56	2.72	0.30	0.067
%	7.4	7.6	5.4	5.4	6.4
Bole wood	80.73	48.21	21.08	2.05	0.297
%	68.0	65.7	41.6	36.7	28.1
Cones	0.74	0.49	0.35	nil	nil
%	0.6	0.7	0.7		
Sum of component weights	118.58	72.90	50.73	5.64	1.051
Total tree weight	118.76	73.41	50.73	5.58	1.181
Total weight 95%	113.20	67.71	47.05	5.26	1.149
confidence limits	- 124.60	- 79.60	- 54.70	- 5.97	- 1.215

(d) Amounts of branch material removed in pruning

Although pruning is an integral part of the management operations in the study area, the artificial removal of the lower branches confuses the pattern of stand development for comparative purposes. The amounts of leaves and branch wood removed during pruning can be estimated from the amounts of material present on the lower boles of trees in the unpruned 7 year old plot 3.

Branches of radiata pine arise in whorls of which the spring whorl is usually most strongly developed. The internode between the spring whorl and the next above is also usually the longest for that year. Consequently the pruning operation frequently removes all branches from several years growth of the main stem and leaves all branches of subsequent years intact.

When the sample trees were collected in plot 3 the dry weights of leaves and branch wood of the branches which would be removed in later pruning were recorded. The size of trees at time of sampling was only generally related to their size 3 - 4 years previously when the basal branches were developing, and there were changes in the competition pattern to which these branches were exposed during this time. Consequently, the relationship between weights removed from a fixed height along the bole and bole size is less precise than the relationship for total crown weights and bole size.

An estimate of leaf and wood weights removed by pruning to a height of 3 m at age 7 years has been obtained from the average weight of prunable material for the nine sample trees in plot 3. The estimate is not critical to the study and is used only to illustrate the pattern of canopy development. Estimates of total foliage and branch weight based on the average for the nine sample trees are less than the estimates derived from regression analysis, and the average diameter of the nine sample trees (11.0 cm)

is less than the plot average diameter (12.3 cm). Estimates of prunable material are possibly also underestimates.

Average dry weight of branch material per tree of plot 3:

of branch wood = 6.27 kg

of branch needles = 3.05 kg

Weight per hectare of prunable material

Branch wood 1.5×10^3 kg

Branch needles 0.7×10^3 kg

2.3.3 Increase in stand dry weight through age series

The pattern of dry weight increment through the age series is shown for the major components separately in Figs. 2.9 and 2.10, and for the whole tree in Fig. 2.11.

(a) Foliage Development

Annual leaf production has been estimated (Table 2.11) from measurements of total leaf weights within the five stands and assuming an average leaf life of three years. The estimated values may be imprecise but the pattern of the model is established by the measured values occurring through the table and can be checked against data from other sources; for example, the values for leaf production in years 3 and 10 should be similar to values for litter fall in the years ending 6 and 13 years, and in fact the production estimates compare reasonably closely with the actual weight of litter collected in the stands of these later ages (Chapter 3.3).

Fig. 2.9, prepared from Table 2.11, illustrates the pattern of leaf development in the study area, the predicted pattern without pruning and the estimated total amount of foliage produced. The pattern of foliage biomass development is very similar to that described for a number of other species (in Tadaki, 1966; Kira and Shidei, 1967), although maximum leaf weight occurs sooner in the present

FIG. 2-9 DRY WEIGHT INCREASE OF CANOPY COMPONENTS WITH AGE IN A P.RADIATA PLANTATION

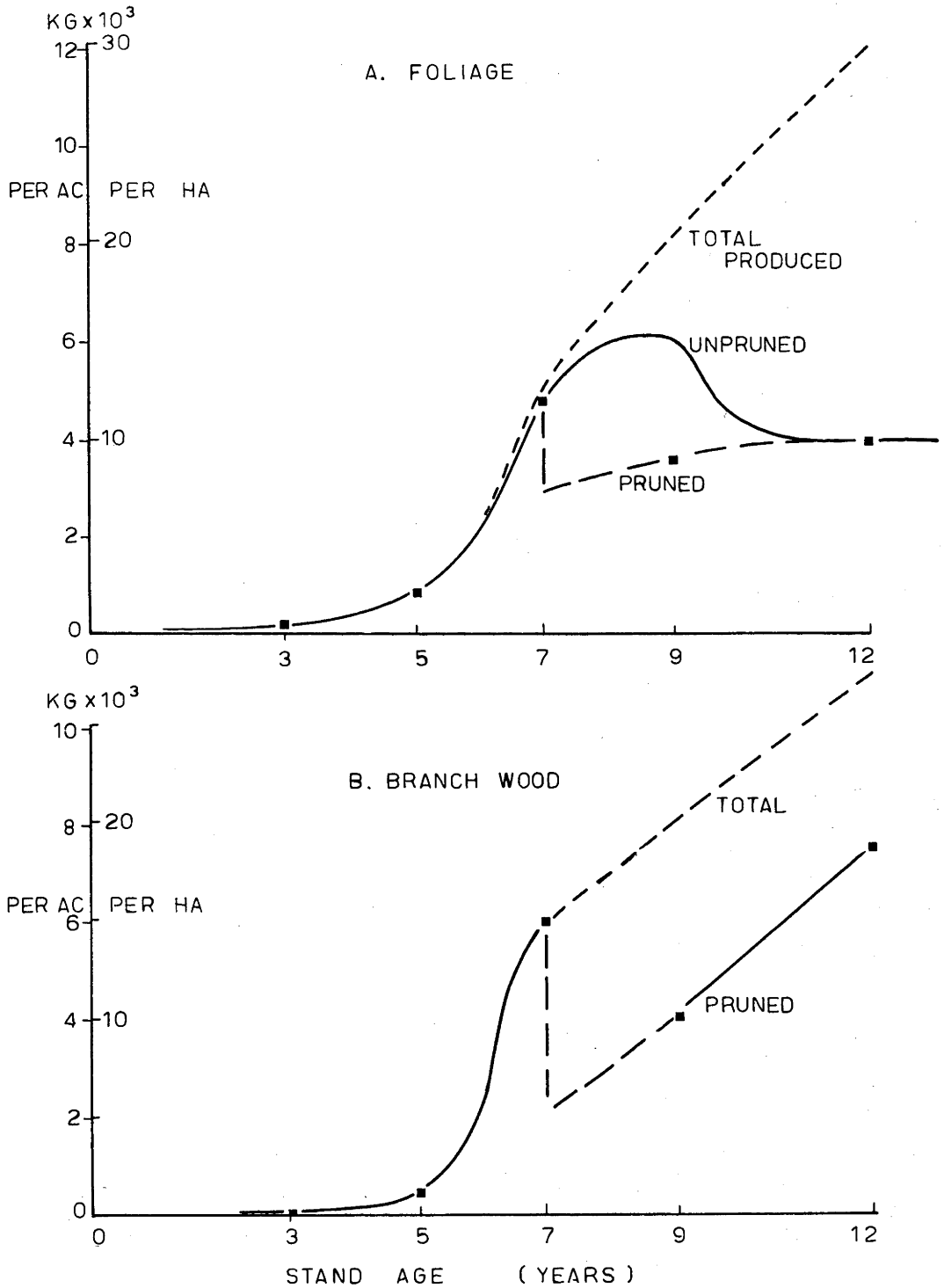


FIG. 2-10 DRY WEIGHT OF BOLE COMPONENTS AT DIFFERENT AGES OF A P.RADIATA PLANTATION

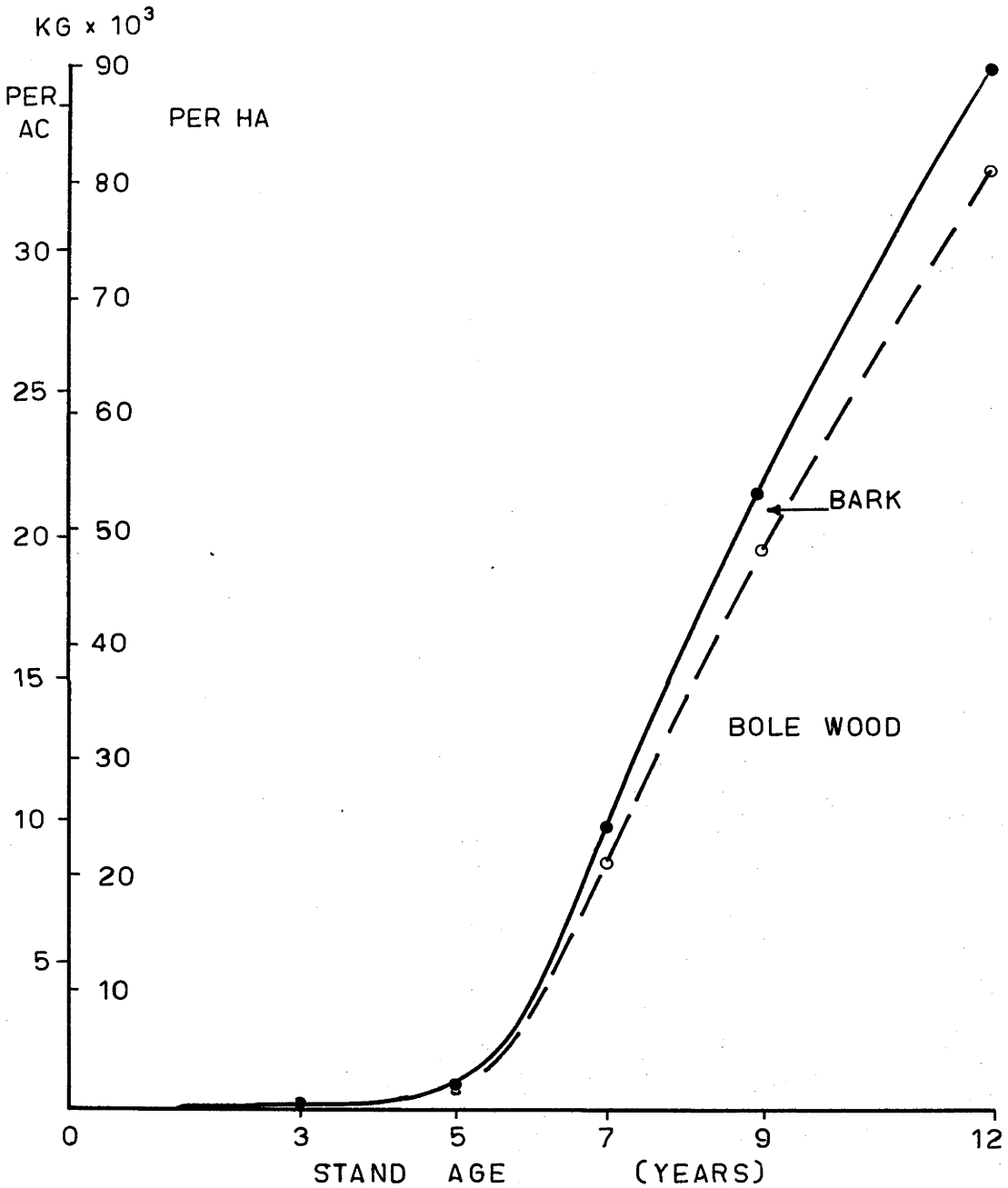


FIG. 2–11 TOTAL TREE DRY WEIGHT AT DIFFERENT AGES OF A P.RADIATA PLANTATION

(ABOVE GROUND)

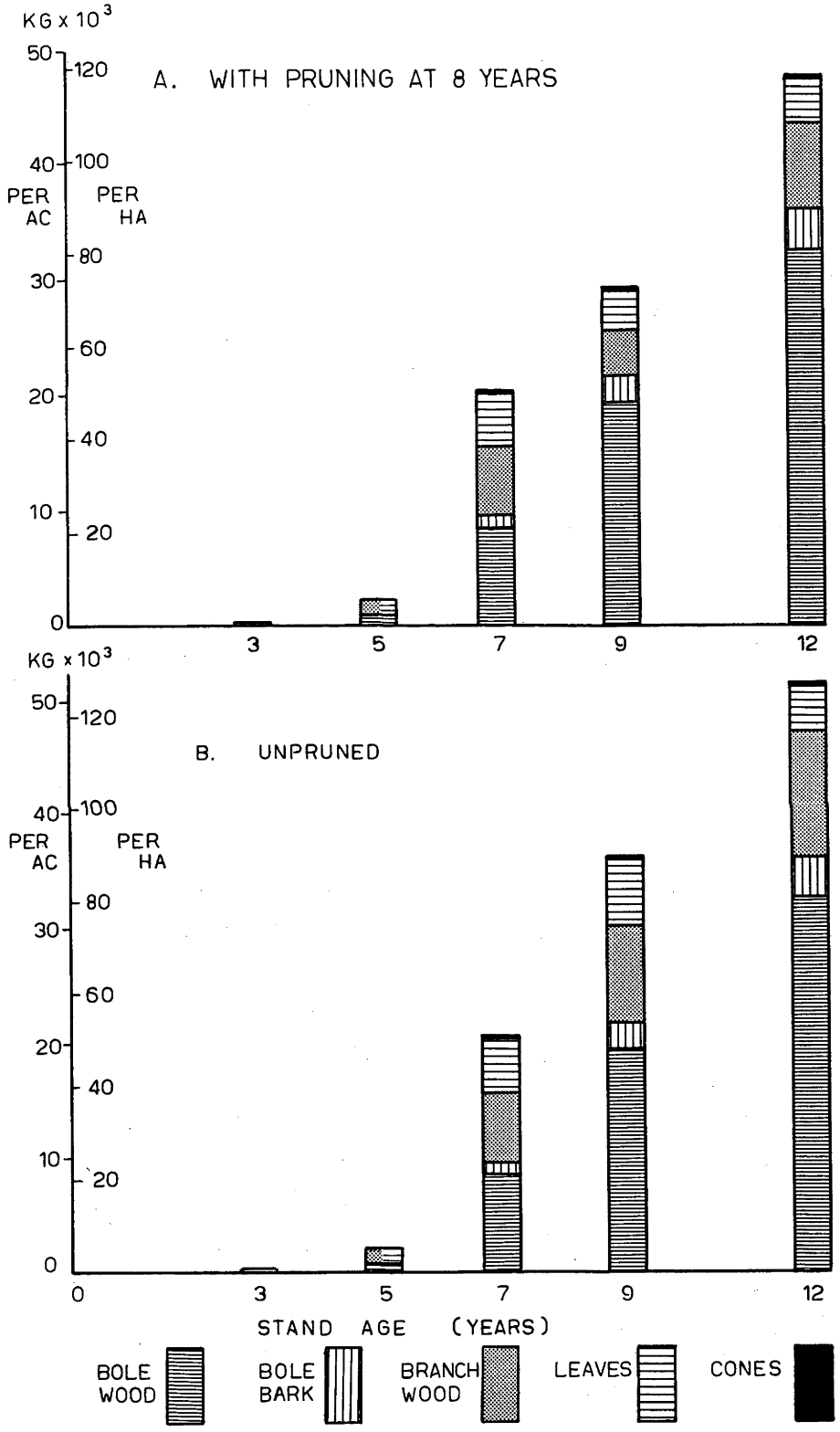


TABLE 2.11 Estimates of total weight of foliage produced in P. radiata age series
(kg x 10^3 per ha)

Year ending (age)	Leaf weight produced during year	Leaf weight on tree		Weight shed during year if 3 yr life	Cumulative total weight produced
		pruned	unpruned		
1	0.05		0.05		0.05
2	0.15		0.15		0.20
3	0.32		0.52 ++		0.52
4	0.57		1.04	0.05	1.09
5	1.21		2.10 ++	0.15	2.29
6	2.55		4.33	0.32	4.84
7	7.90		11.66 ++	0.57	12.74
8	3.88	8.03	14.33	1.21	16.62
9	3.05	8.70 ++	14.83	2.55	19.67
10	3.20	9.02	10.13	7.90	22.87
11	3.14	9.39	9.39	3.88	26.01
12	3.30	9.59 ++	9.64	3.05	29.31

++ = measured values.

study and the peak is more pronounced because of the very rapid growth from age 5 years to full canopy closure at 8 years. The peak in stand foliage weight results from the rapid expansion of tree crowns immediately before canopy closure. Between 6 and 7 years, tree crowns expand rapidly both vertically and laterally and the stand foliage weight increases by nearly 8,000 kg per ha; after this age further lateral expansion is restricted by between-tree competition and the rate of new foliage growth is not more than 4,000 kg per ha per annum (Table 2.11). By 9 years the total weight of foliage approaches 15,000 kg per ha but by the end of that year the mass of leaves grown during year 7 are shed. Thereafter the growth of new foliage is balanced by shedding of the old, and the total weight of leaves per hectare then remains more or less constant at about 10,000 kg.

After 12 years the weight of foliage is probably constant at about 10 metric tons per ha with annual recruitment and shedding of about one-third of this amount, i.e. 3 m tons per ha. This value for foliage weight is at the upper limit of the range 2.8 - 10.5 m tons per hectare of leaf biomass given by Tadaki (1966) in a summary of seventeen separate studies of pine forests around the world, and is close to the value (9.0 m tons per ha) reported by Will (1964) for P. radiata in New Zealand. The rate of foliage turnover is also within the range reported for similar forest stands (Bray and Gorham, 1964); litter fall is examined more closely in Chapter 3.

(b) Branch wood development

Branch wood weight increases at about the same rate as foliage weight (Fig. 2.9) except that without regular shedding there is a continuing increase in live branch wood material from 9 to 12 years of 3.05 m tons per ha per annum, but this is very much less than the peak production of nearly 10 m tons per ha from 6 - 7 years.

Although radiata pine is not self pruning in this environment, the lower branches progressively die and decay so even without manual pruning in the older stands of the age series the total weight of branch wood remaining on the trees would have been less than the total weight of branch wood produced.

Although more data are needed to estimate the development rate of live branch wood and dead branch wood separately, the total weight of branch wood measured for plot 1 is almost completely of live material, but one year later the lowest branches on most trees were dead. Branch wood weight in plot 1, 18.5 m tons per ha, is probably near the maximum weight of live branch wood contained in P. radiata stands in this locality at this spacing. Decrement by death, but not necessarily shedding, would then balance increment by growth in the tree apex and of older living branches. This estimate of branch weight is considerably greater than the value estimated by Will (1964) for radiata pine in New Zealand of the same age, but the stands there had a much greater stand density (2644 stems per ha). Unlike leaf weights, branch wood weight per unit area is probably density dependent because of the continued growth in thickness and length of lower branches with lighter stocking; this was not the case with the more tolerant balsam fir (Baskerville, 1965a), but Satoo (1967a) showed the branch biomass of P. densiflora decreased markedly with increased stand density, particularly through the range 1000 - 4000 stems per ha.

(c) Bole development

Before age 5 years the rate of bole development is small, but after that time both bole wood and bole bark weights increase relatively regularly at 12 and 1.3 m tons per ha per annum respectively (Fig. 2.10). There is little evidence of a marked peak in the production of either bole

wood or bark before age 12 years, although increment between ages 7 and 9 years (14.8 m tons per ha per annum) is slightly greater than in the following three years (11.9 m tons per ha per annum). From an analysis of the growth of a radiata pine stand over 30 years on a slightly better quality site in New Zealand, Spurr (1962) concluded maximum volume production occurs at about age 20 years, and Will (1964, 1966a) accepted this conclusion in estimating maximum dry weight production for similar stands.

The total weight of foliage is at a maximum for unpruned P. radiata stands at about 8 - 9 years, but this maximum is not so marked in stands pruned soon after canopy closure. Because of the marked decline in photosynthetic activity of leaves older than 2 years (Wood, 1968) maximum carbohydrate assimmilation would be expected in the study area 7 or 8 years after planting. Neither branch nor leaf production is greater at this time than in other years and so bole production is probably at a maximum before the 10th year. The efficiency of transpiration and photosynthesis might also decrease and the respiration: photosynthesis ratio increase as the canopy height increases, tending to reduce overall leaf efficiency and total production with tree age.

Data presented by Spurr (1962) indicate maximum bole volume production on living trees (net current annual increment) occurred before or during the first year of his study when the trees were 9 years. Gross increment, assessed as the difference between total standing volume of all trees both living and dead in successive years, was at a peak at 9 years (50 cu m per ha) and this value was exceeded in only 2 years, ages 20 - 21 years, after one-third of the initial 1525 stems per ha had died in the preceeding eight years. The second peak in Spurr's data probably results in response to stimulated crown development in remaining trees after many in the stand had died; the recovery to full

canopy closure of the remaining trees would reproduce the conditions prevailing before the crowns first closed.

The final rate of bole wood production estimated in this study (10.8 m tons per ha per annum) compares well with the level of wood volume increment (28 cu m per ha = 400 cu ft per ac) expected in plantations of this quality if an average wood density of 0.40 gm per cc (25 lb per cu ft) is assumed (Lewis, 1962; Fielding and Brown, 1960).

(d) Root development

Only the above-ground parts of sample trees in the age-series were harvested, but tentative estimates of root development can be made from reference to other studies.

Tree roots (>0.5 cm) in the 8-year old 100-tree plot (Chapter 1) weighed 10.6 m tons per ha, contributed 16% of the total stand weight and were 19% of the total weight above ground. In contrast, Will (1966a) estimated the dry weight of the root mass in an 18-year old P. radiata stand to be 33 m tons per ha or 11% and 12% of the total and above-ground weights respectively.

Lateral root extension is restricted by physiological and physical factors. After the initial establishment of trees, most of the dry weight increase of the root system of a forest stand is probably in the stump, tap root and a few thick lateral roots. The tree canopy weight increases slowly after crown closure, so the root: canopy ratio probably increases with age; however net root production is unlikely to be maintained at a high level for as long as bole production so the root: bole ratio probably decreases. The production rates estimated by Will (1966a), although very approximate, support these possibilities. It is likely then that the ratio of below ground weight to total weight varies little with stand age. Bray (1962) has also reached this conclusion from an analysis of production for several tree species.

The ratio of root to total stand weight is greater in the 100-tree plot (16%) than in the better site quality, older stand (11%). This is at least consistent with the frequent observation in seeding nutrient culture studies that root: shoot ratios may decrease with increasing fertility in the growth medium (for example, see Chapter 9).

The proportion of the total biomass in the roots varies markedly between vegetation types; for grasses and herbaceous species much of the biomass may be below ground, but the proportion of below-ground material usually decreases as the above ground parts becomes taller (Bray, 1962). The proportion of biomass below ground possibly varies relatively little between widely contrasting productive forest stands. For example, data presented by Rodin and Bazilevič (1966) shows the proportion of roots in a wide range of forest types vary from 18 to 26% of the biomass (Table 2.12); and Young and Carpenter (1967) have calculated the roots of single 10 m (35 ft) high saplings of four broad leafed and four conifer species to range from 14.6 to 23.2% of total sapling weight.

TABLE 2.12 Proportion below ground of total biomass from Rodin and Bazilevič (1966)

Vegetation type	Biomass (m tons/ha)	Percentage below ground
Northern spruce forest	100	22
Central spruce forest	260	23
Southern spruce forest	330	22
Beech forest	370	26
Oak forest	400	24
Subtropical broadleafed	410	20
Moist tropical forest	500	18

The available data indicates root weight is a smaller proportion of total biomass in P. radiata plantations than in many other productive forest stands. If root weights in the older plots of the age series are assumed to be 15% of the total biomass, the following weight estimates result, but they could be subject to considerable error.

	Plot 3 7 years	Plot 2 9 years	Plot 1 12 years
	(metric tons per ha)		
Total above ground	51	75	120
Root mass	9	13	21
Total biomass	60	88	141
Annual production			
of roots	2	3	
of biomass	14	18	

The values estimated for root dry weight production do not include the annual turnover of fine roots, which may be considerable.

2.3.4 Dry weight of subordinate vegetation

The dry weights of ground vegetation in the five plots of the age series are shown in Fig. 2.12 and by species groups in Table 2.13. The native grasses and some other vegetation of the original sclerophyll forest had survived the pre-planting clearing and burning mainly because of their capacity to regenerate from subterranean organs. These plants were thus able to take full advantage of the release from competition.

FIG. 2-12 DRY WEIGHT OF ORGANIC MATTER TYPES IN P. RADIATA PLANTATIONS

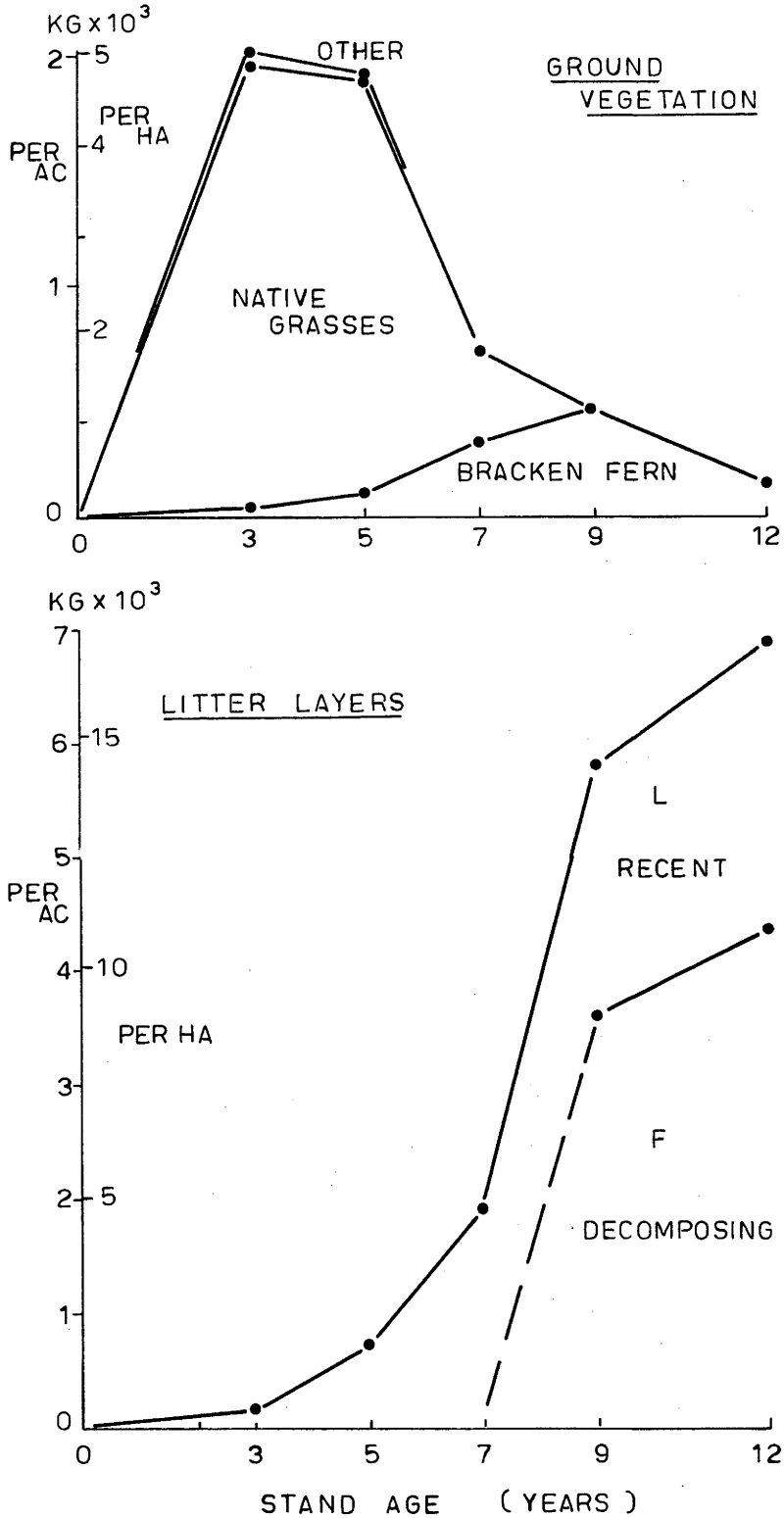


TABLE 2.13 Dry weight of ground vegetation and litter layers of *P. radiata* age series

Ground layer component	Total weight in twenty x 1/ 16 sq m quadrats (gms)	Number of quadrats with material	Total dry weight (m tons/ha)
Plot 1 Age 12 yrs			
Ground vegetation			
Bracken fern	48.7	4	0.40
Litter layer			
Pine leaves	617.1	20	4.94
Pine branch wood	163.7	12	1.31
Decomposing	1353.1	20	10.82
Total	2182.6	20	17.47
Plot 2 Age 9 yrs			
Ground vegetation			
Bracken fern	145.5	11	1.16
Litter layer			
Pine leaves	326.1	20	2.62
Pine branch wood	356.1	12	2.84
Decomposing	1113.0	20	8.90
Total	1940.7	20	15.52
Plot 3 Age 7 yrs			
Ground vegetation			
Bracken fern	104.4	4	0.84
Native grasses	123.0	16	0.99
Litter layer			
Total	590.5	19	4.72
Total	817.9	20	6.55
Plot 4 Age 5 yrs			
Ground vegetation			
Native grasses	551.2	18	4.42
Bracken fern	36.3	2	0.30
Broad-leaf weeds	13.7	4	0.10
Litter layer			
Total	228.4	16	1.83
Total	829.6	20	6.65
Plot 5 Age 3 yrs			
Ground vegetation			
Native grasses	597.9	18	4.79
Bracken fern	15.1	1	0.12
Broad-leaf weeds	18.3	2	0.15
Litter layer			
Total	54.1	3	0.42
Total	685.4	19	5.48

An inspection of many freshly burned plantation areas showed a small but extremely variable ground flora, nevertheless, it was assumed that immediately after the clearing burn and at the time of pine planting (i.e. age 0 years) subordinate vegetation was absent. The native grasses develop rapidly and at age 3 years amounted to 5 m tons per ha. At 5 years the quantity of native grasses was slightly less than at 3 years, but the bracken fern was becoming abundant. The closing of the pine canopy after 5 years results in the immediate suppression of the grasses, which occur only occasionally in well developed stands, usually in gaps in the canopy. Bracken fern develops slowly at first but seems less sensitive to competition than the grasses. By 9 years bracken fern amounted to 1.2 m tons per ha. At 12 years only 400 kg per ha of understory vegetation was present, and this was typical for closed-canopy stands generally.

The rapid degeneration of the grasses, and to a lesser extent of the bracken fern, is probably hastened by the smothering action of the pine leaf litter fall which is substantial after 7 years (Chapter 3.3.2).

2.3.5. Dry weight of the litter layer

The litter layer in plots 3 to 5, up to age 7 years, consists of fragmented remnants of grass tussocks, bracken fern, woody plants and occasional pine neddles; and these are difficult to separate. Some decomposition had taken place but the small amount of decomposed material had been immediately incorporated with the mineral soil surface. Over much of the forest floor there were bare patches devoid of organic matter, particularly in the younger plots, one of the 20 quadrat placements in plot 5 being completely bare of litter or living vegetation.

The dead organic matter on the forest floor of plots 1 and 2 was distinctly two layered. The top (L) layer of

recently fallen material was mainly pine leaves shed when between 3 and 4 years old, but also in plot 2 there were younger leaves and branch wood which had been prematurely removed in the pruning at age 8 years. This upper (L) layer was readily distinguished from the amorphous fragmented and decomposing material (F and H) beneath. The lower layer, which amounted to 10.8 m tons per ha by age 12 years, comprised initially both dead remains of pine and non-pine vegetation, but with increasing plot age pine foliage contributed an increasing proportion.

Initially decomposition rates are small, probably partly due to the small microbial population adapted to the breakdown of the exotic pine material. Soon after full canopy closure, the establishment of a more or less uniform environment below the forest canopy and a relatively constant litter fall, the rate of decomposition reaches equilibrium with litter fall. Many stands ranging up to 35 years old and adjoining the study area were examined, but in none was the litter layer thicker than in study plot 1 (12 years old). There are insufficient data from the older stands to fully describe litter layer development, breakdown and mineralization, but observation within the study area and elsewhere (R. Florence, pers. comm.) suggests the levels of 10.8 m tons per ha of decomposing material and 5.0 m tons per ha of freshly fallen, undecomposed material present at age 12 years are close to the maximum occurring under P. radiata in this locality.

The total amount of organic matter per hectare returned to the forest floor by age 12 years is estimated as 20 m tons of pine foliage (Fig. 2.9a), 10 m tons of pine branch wood (Fig. 2.9b), 1.7 m tons of pine male cones (Chapter 4), and 7.5 m tons of subordinate vegetation (including that removed in cleaning operations and not assessed) i.e. a total of 39.2 m tons, of which approximately 32 m tons is deposited per hectare during the five years from ages 7 to 12 years.

The total amount of litter present at 12 years is estimated at 17 m tons per ha, so the average rate of litter reduction (by incorporation, mineralization, animal consumption etc) over the five year period was 3.0 m tons per ha. Probably the rate of litter reduction increases during the five year period, but at the end of the period (at age 12 years) annual litter fall is 3.2 m tons per ha (Table 2.11, see also Chapter 4). These figures support the observation that a balance between litter accumulation and reduction is established soon after age 12 years under the conditions prevailing in the study area.

2.4 DISCUSSION - STAND DRY WEIGHT ACCUMULATION

2.4.1. Total Dry Weight accumulation through age series

The dry weight of all organic matter present above ground level on the five study plots of the radiata pine plantation is summarised in Table 2.14. The five study plots have been shown to represent, within the limits of practicability, five successive stages of a single stand, and the development of total dry weight within such a hypothetical stand is shown in Fig. 2.13.

The overall development pattern through the age series results from the development of the four major above-ground layers within the ecosytem, i.e. the tree crown/canopy layer, the tree boles, the subordinate vegetation and the litter layer on the ground surface. Each major layer has its characteristic development pattern, but these are not mutually independant. The development of the tree canopy layer effectively determines the rate of development of the other three zones; bole wood production is directly related to the photosynthetic capacity of the canopy layer, litter layer development is controlled directly by regular shedding of material primarily from the tree canopy and indirectly through the influence of the canopy in maintaining a uniform

FIG. 2-13 TOTAL DRY WEIGHT OF ORGANIC MATTER ABOVE GROUND WITH AGE IN A P. RADIATA PLANTATION

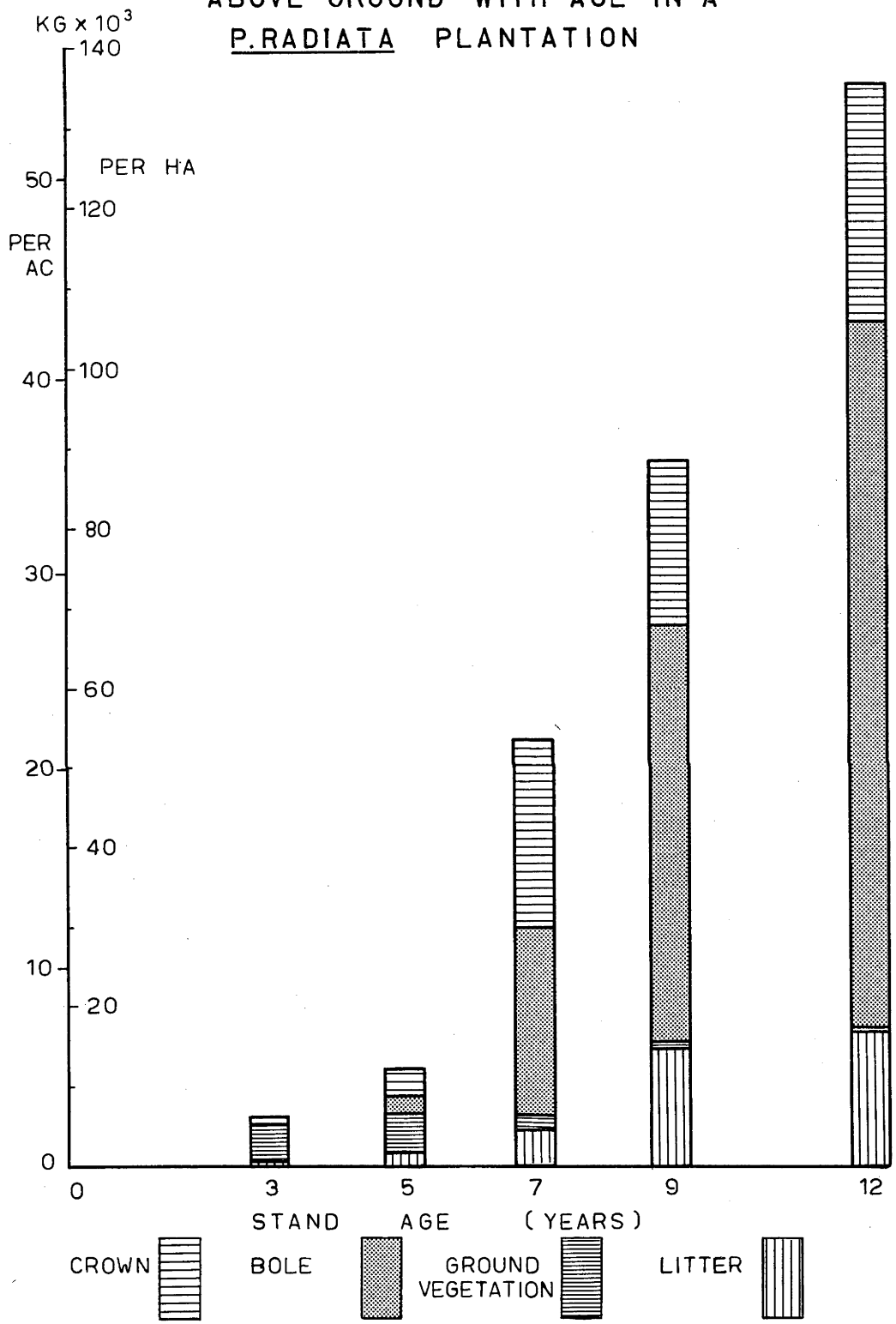


TABLE 2.14 Total dry weight above ground in a P. radiata age series (m tons per hectare)

	Study plot Number / Age				
	5	4	3	2	1
	3 yrs.	5 yrs.	7 yrs.	9 yrs.	12 yrs.
Branch wood	0.17	1.20	14.92	9.91	18.73
Leaves	0.52	2.09	11.66	8.73	9.57
Cones	-	-	0.35	0.49	0.74
Total crown	0.69	3.29	26.93	19.13	29.04
% of total above ground	10.6	27.6	47.1	21.7	21.4
Bole wood	0.30	2.05	21.08	48.21	80.73
Bole bark	0.07	0.30	2.72	5.56	8.81
Total bole	0.37	2.35	23.80	53.77	89.54
% of total above ground	5.6	18.9	41.5	60.8	65.8
Total tree by addition	1.05	5.64	50.73	72.90	118.58
by regression	1.18	5.58	50.73	73.41	118.76
% of total above ground	16.2	45.6	88.6	82.5	87.2
Ground vegetation	5.06	4.82	1.82	1.16	0.40
% of total above ground	77.4	39.5	3.2	1.3	0.3
Litter layers	0.42	1.83	4.72	14.36	17.07
% of total above ground	6.4	14.9	8.2	16.2	12.5
Total subordinate	5.48	6.65	6.55	15.52	17.47
Total above ground	6.66	12.23	57.28	88.93	136.23

and suitable environment for breakdown and decomposition to occur, and the subordinate vegetation responds inversely to canopy spread and competition.

The percentage distribution of dry weight between the major layers at each age (Fig. 2.14) also illustrates the importance of initial rapid crown development. By age 7 years crown components contribute nearly 50% to the total above ground dry weight. Afterwards only bole components increase substantially and by age 12 years make up 66% of total dry weight.

2.4.2 Dry weight increment through age series

Dry weight increment through the age series has been calculated by dividing the difference in weight between successive periods by the time interval (Table 2.15, Fig. 2.15). The slight overestimate of pine component increment for the 0 - 3 years period incurred by assuming nil weight at time 0 is unimportant because the increment is small compared with the increment for later periods. (Average weight of seedlings used for planting in 1966 was 6.2 gms, of which the stem weighs 1.4 gms and the foliage 3.4 gms; i.e. total weight above ground of seedlings planted at 1680 per ha = 7.9 kg).

Maximum increment (22.5 m tons per ha per annum) occurs between ages 5 and 7 years, when the increment of the crown components approaches 12.5 m tons per ha per annum and of bole components is only slightly less. During the next two year period the total weight of crown components would normally either increase only slightly or decrease because of the heavy fall of three year old leaves which had been produced immediately prior to full canopy closure. Under the conditions of this study the decrease in crown weight was increased by the pruning of live branches.

FIG. 2-14 DISTRIBUTION OF DRY ORGANIC MATTER IN THE MAIN ABOVE-GROUND LAYERS OF A P.RADIATA PLANTATION

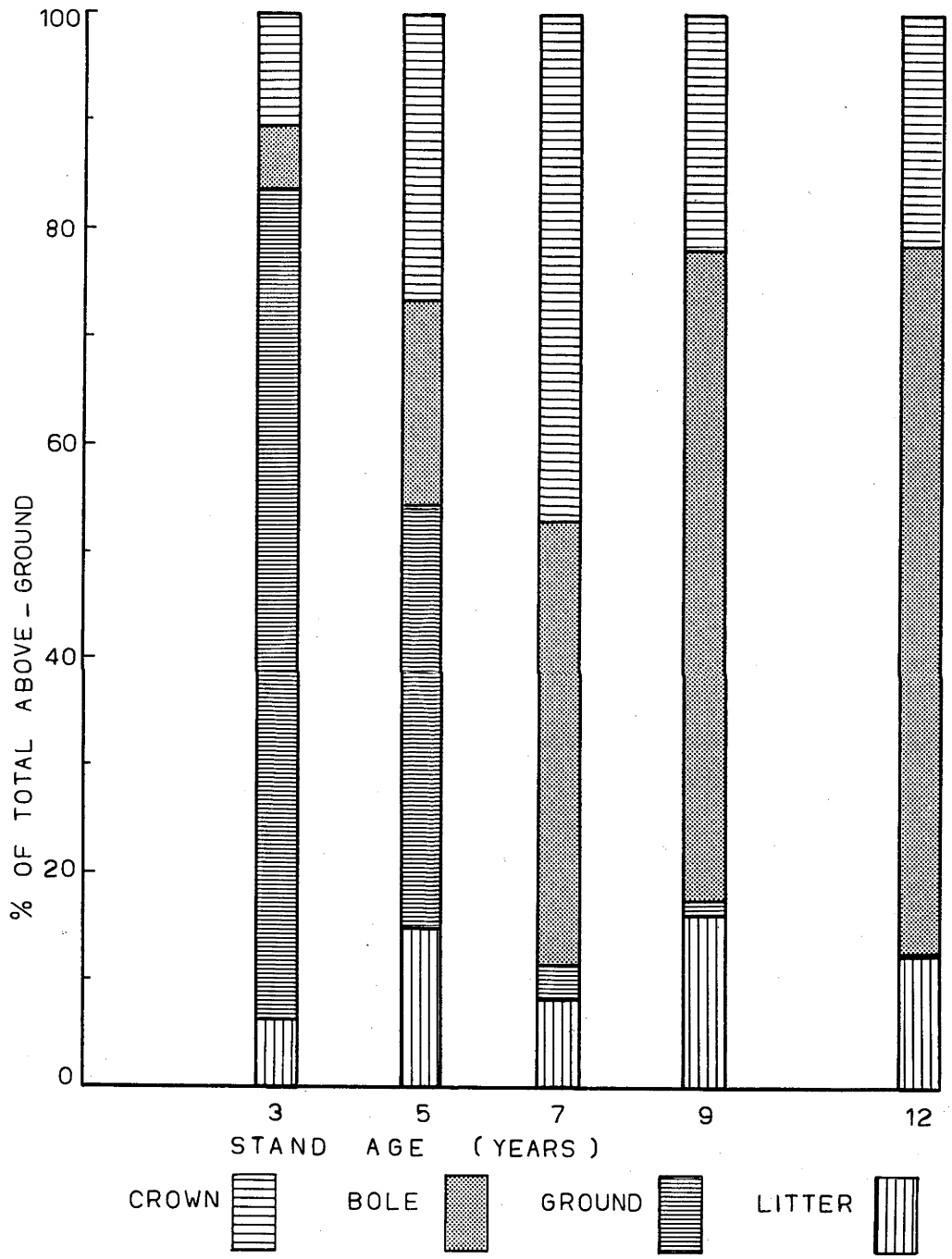


FIG. 2-15 DISTRIBUTION OF DRY WEIGHT INCREMENT IN THE MAIN ABOVE GROUND LAYERS OF A P.RADIATA PLANTATION

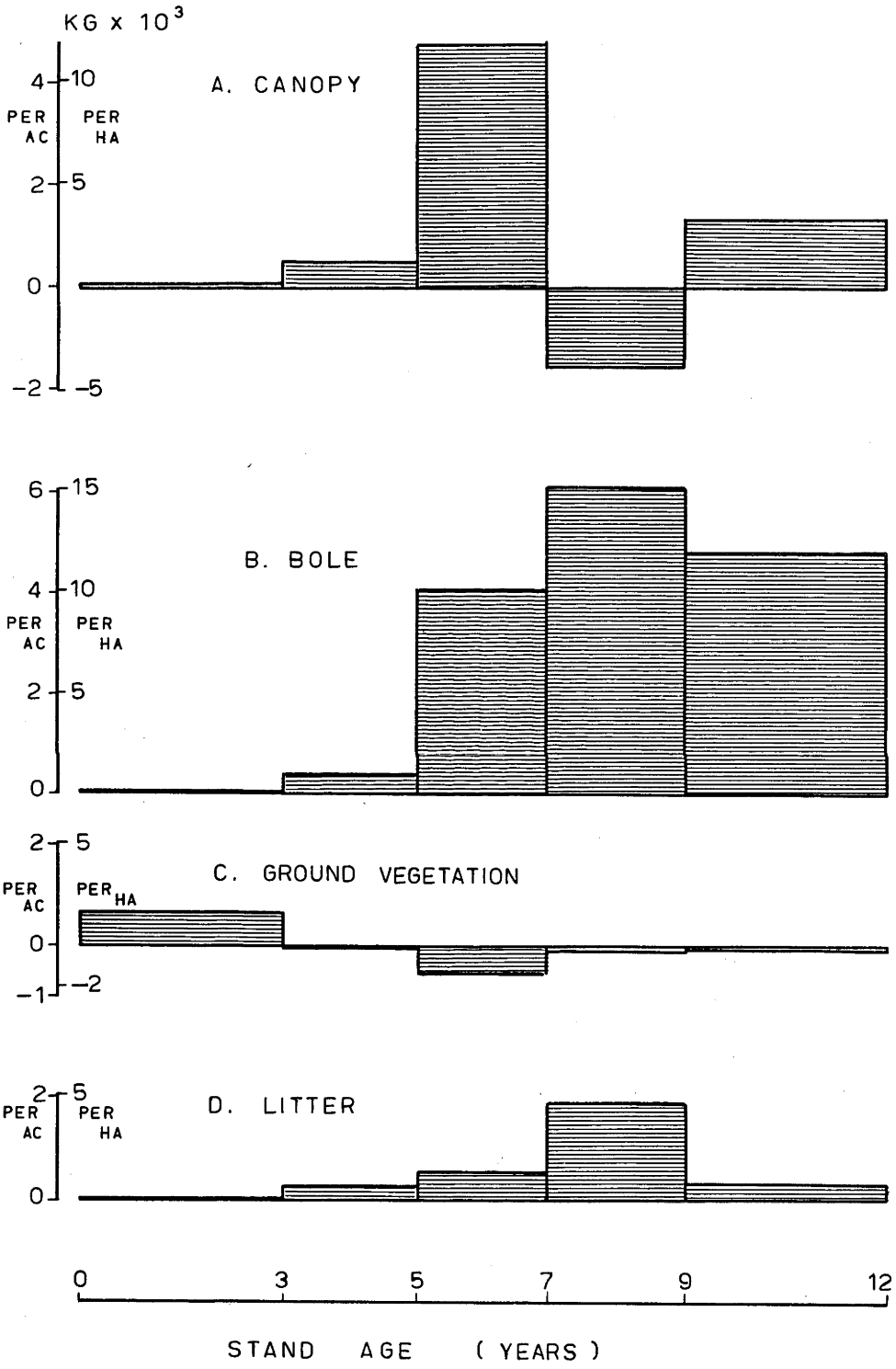


TABLE 2.15 Distribution of dry weight increment within a *P. radiata* age series (m tons per hectare per annum)

Component	Stand age (years)				
	0 - 3	3 - 5	5 - 7	7 - 9	9 - 12
Branch wood	0.05	0.52	6.87	-2.50	2.94
Leaves	0.17	0.79	4.79	-1.48	0.30
Cones	-	-	0.17	0.07	0.07
Total crown	0.22	1.31	11.83	-3.91	3.31
% of total above ground	10.1	46.0	52.4	-24.6	20.9
Bole wood	0.10	0.86	9.51	13.57	10.85
Bole bark	0.02	0.12	1.21	1.43	1.09
Total bole	0.12	0.98	10.72	15.00	11.94
% of total above ground	5.6	34.7	47.7	94.7	75.6
Total tree	0.34	2.28	22.55	11.34	15.12
% of total above ground	15.7	79.2	100.1	71.7	95.9
Ground vegetation	1.68	-0.12	-1.48	-0.35	-0.25
% of total above ground	77.3	-4.4	-6.5	-2.2	-1.6
Litter layers	0.15	0.72	1.43	4.82	0.89
% of total above ground	6.8	25.2	6.4	30.4	5.6
Total subordinate	1.83	0.60	-0.05	4.47	0.64
% of total above ground	84.3	20.8	-0.1	28.2	4.0
Total above ground	2.17	2.88	22.50	15.81	15.76

Production beyond age 10 years is virtually confined to the woody components of the tree crop. Ground vegetation is almost eliminated, and leaf production, shedding of 3 year old leaves, and litter decomposition and incorporation have reached an approximate dynamic balance. Branch wood production is estimated at 2.5 m tons per ha per annum although this depends on the rate of dead branch decay and shedding which has not been assessed; total bole production is constant at about 12.5 m tons per ha.

These production rates compare closely with the values estimated by Will (1964) for a fully stocked second rotation radiata pine stand in New Zealand of similar site quality.

2.4.3. The effect of site quality on dry weight production

The present study was made in a very productive stand of P. radiata, probably better than the average for plantation stands in Australia. However the data can be extrapolated, together with data from other sources, to give a reasonable prediction of growth on other sites. This is valuable in the context of this thesis particularly in later discussions of the effects of fertilizer addition on growth behaviour because nutrient deficiencies usually occur on much poorer sites then those examined.

All the available data indicate a relatively uniform weight of foliage in radiata pine stands after canopy closure over a wide range of site conditions. In the older stands of the present age series (S.Q. III) the foliage weight is 10,000 kg per ha, which was also obtained in the 100-tree (S.Q. V) plot (Chapter 1) at canopy closure, and is only slightly greater than obtained by Will (1964) for S.Q. II natural regeneration. Results of litter fall studies by Pawsey (1959) for S.Q. III stands in South Australia, Hamilton (1964) for a range of sites in the A.C.T. and Will (1959) for three stands in New Zealand all show rates of litter fall remarkable similar to that in the

present study (see Chapter 3 for details) indicating similar live foliage levels at each of these localities. Satoo (1967a) has also shown foliage weight in P. densiflora plantations to be relatively independent of both stand age and site quality over a wide range of both.

The effect of site quality is reflected in young plantations in the rate of canopy development and the time taken to reach full closure and maximum weight. In the age series, S.Q. III stands reached canopy closure in 7 years but S.Q. I stands may achieve a similar stage of development in only 5 years, while S.Q. V stands may take 10 - 12 years.

After full canopy development total production rates differ widely on contrasting sites; if foliage levels are as uniform as the data suggest then site must have a substantial influence on the overall photosynthetic capacity of the foliage present. Shepherd (1967) has indicated the ability of P. radiata to grow whenever soil moisture and temperature remain favourable, but inadequate water supply is a contributing cause of poor growth on many sites. Wood (1968) has shown photosynthesis and assimilation to be markedly reduced under conditions of water stress, and during extended dry periods respiration may more than balance photosynthesis. From data presented by Wood (1968) it seems that under conditions of stress for either water or nutrients the period may be reduced over which leaves retain optimal photosynthetic capacity before entering a period of decline and ultimately death. Thus while the total weights of leaves of each age class may be similar in stands of different site quality, the period during the growing season for which the leaves will be photosynthetically active will undoubtedly be less on sites where stress is imposed, the decline in activity of leaves may begin earlier in their three year life span, whilst under some conditions the life span may be reduced.

Data of branch wood growth and the effects of site differences are meagre compared with that for foliage, and comparisons of data from various sources is further confused by the apparent influence of stocking rates on branch wood growth. For example, in 8-year old S.Q. V stands and 12-year old S.Q. III stands the weight of live branch wood is 16.8 and 18.7 m tons per ha respectively, while the 12-year old S.Q. II stands with almost double stocking rate had only 7.8 m tons per ha (Will, 1964). After examining a wide range of P. densiflora stands, Satoo (1967a) concluded the total weight of branch wood increased regularly with age but was very dependent on stand density, particularly at stocking rates below about 4,000 stems per ha.

Will (1966a) reported only total branch wood weight and leaf weight for an 18-year old S.Q. I P. radiata stand which had been thinned 10 years previously to about 700 stems per ha, but if foliage weight is assumed to be 10,000 kg per ha then the branch wood weight of the stand is 29 m tons per ha.

Thus, branch wood weight per unit area is probably more dependent on initial stocking rates than on moderate differences in site quality. In older stands the nature and intensity of thinning will also contribute largely to differences in branch weight. However, it would seem live branch wood weight per unit area varies only little with site quality, being generally greater in stands of higher site quality. The amount of dead branch wood may be greater in higher site quality stands because of greater total production, but this would also depend on the rate of branch wood decomposition.

The effect of site quality is most apparent in relation to the growth of the tree bole. Few data are available for the effect of site on bark thickness, but over the range of sites and ages of the studies referred to previously, the proportion of bark to total bole remains relatively constant at about 10 - 12%, although decreasing slightly with stand

age. Consequently, the bole can be discussed as a single unit.

The bole volume data of Jacobs (1962), Spurr (1962), and Keeves (1966) when converted to weight agree closely with the weights of bole wood in plots of the age series (S.Q. III) and the 100 - tree plot (S.Q. V). (For conversion of volume to weight, an average tree wood density of 0.40, 0.42 and 0.45 gm per cc was assumed for stands of 10, 15 and 20 years respectively - P. Rudman, pers. comm.). So the dry weight data can be extrapolated for stands of greater age and other site qualities using the volume data.

The effect of site quality on root production is not known, but it seems likely from previous observations (Chapter 2.3.3.d) the proportion of total dry weight production going to roots decreases with increasing site quality. The individual factors of the environment which are most important at a particular site, for example, water availability, nutrient supply or aeration, probably differ in their effects on root development; so root production particularly, may vary substantially between localities of the same site quality.

Thus, stands of differing site quality differ, not only in bole wood and total dry weight production, but in the distribution of total production. Bole wood increment is probably a greater proportion of the total dry weight increment in stands of better site quality.

2.5 SUMMARY

In managed plantation stands of P. radiata maximum dry weight production will normally occur before 10 years of age. The initial tree spacing usually adopted ensures on all but the poorest sites full canopy development and closure by age 10 years, and this is associated with a peak in stand foliage dry weight. Because photosynthetic capacity

is at a maximum but further canopy expansion is restricted, a peak in bole wood production also normally occurs.

Variation in site quality, initial spacing and degree of non-pine competition will influence the age at which canopy development is complete, and hence the age of maximum production. The situation of massive canopy development and stimulated bole wood production could result from the heavy thinning (and to a lesser extent in some circumstances from substantial deaths) within a fully stocked stand after initial canopy closure, in which case another peak in total production may occur.

For a short time as the canopy closes the weight of foliage, and presumably the stand photosynthetic capacity, is greater than can be produced in closed stands. Total biomass increase over the three year period about canopy closure was 22.5 m tons per ha per annum, and the bole increase was 11 m tons or 48% of the total. Immediately after canopy closure the bole dry weight increased by 15 m tons per ha per annum, but subsequently the bole dry weight increase was 12 m tons and the total stand dry weight increase was 15 m tons per ha per annum.

CHAPTER 3

SEASONAL CHANGES IN DRY WEIGHT OF P. RADIATA FOLIAGE

Contents Page

CHAPTER 3

SEASONAL CHANGES IN DRY WEIGHT OF P. RADIATA FOLIAGE

3.1 INTRODUCTION

In the previous Chapter the dry weights of the main components of several P. radiata stands were examined to estimate the net accumulation of organic matter over successive periods. From these data the rates of development of young stands were determined. However, the dry weight production estimates are based on amounts of organic matter present in each stand at a single sampling time and do not take into account seasonal variations which are known to occur.

Apart from seasonal changes in the overall rate of development, of canopy expansion, bole height and diameter growth, etc., secondary changes of a cyclic nature take place which may have considerable influence on the overall pattern of development.

Seasonal changes in foliage composition are most apparent in deciduous hardwood forests, where full leaf development, death and shedding occur annually. Seasonal changes in the weight and composition of conifer foliage may also be considerable (Tamm, 1955), but the relevance of these changes cannot be appreciated from an examination of the forest stand at only one time in the year. For example, the cycle of growth, maturity and shedding of male cones is completed within a year and failure to recognise flower and seed production may result in an incomplete assessment of total growth (Ovington, 1963). Fielding (1960) has estimated annual male cone production in P. radiata stands at up to 1,000 kg per ha, and 280 kg per ha was collected from the trees of the 100 - tree plot (Chapter 1). When

the sample trees were collected in July - August, male cones were present as immature buds and not collected separately.

Some seasonal changes occurring within the radiata pine age - series have been determined, since an appreciation of their importance seemed desirable for a satisfactory discussion of the main results. Seasonal variations investigations have been mainly confined to foliage changes, in relation to:

(i) changes occurring during the life of leaves, and

(ii) litter fall.

3.2 CHANGES IN LEAF WEIGHT WITH AGE

3.2.1 Methods

During August, 1966, five P. radiata trees were selected for study in the five - year old study plot. Only trees where the annual stages of growth through the crown could be recognised easily were selected, and any abnormal trees were rejected. The height and diameter of each selected tree were close to the plot averages.

Within each tree the branch whorls developed during each of the three previous spring seasons were identified. The leaves on the first internode along these branches from the bole were thus 1 -, 2 - and 3 - years old respectively. Four branches were selected in each of the three whorls, and at the time of selection and on seven subsequent occasions during the next 12 - months, one fascicle of three needles was selected at random from midway along the first internode of each of those four branches and carefully removed; the four fascicles were grouped into a single sample for each whorl. The fascicle sheathes were carefully removed leaving twelve separate needles per sample which were placed in a stoppered glass phial to minimise moisture loss. The fresh weight of each sample was recorded in the laboratory within 24 hours of collection, and dry weights were taken after oven drying at 85° C.

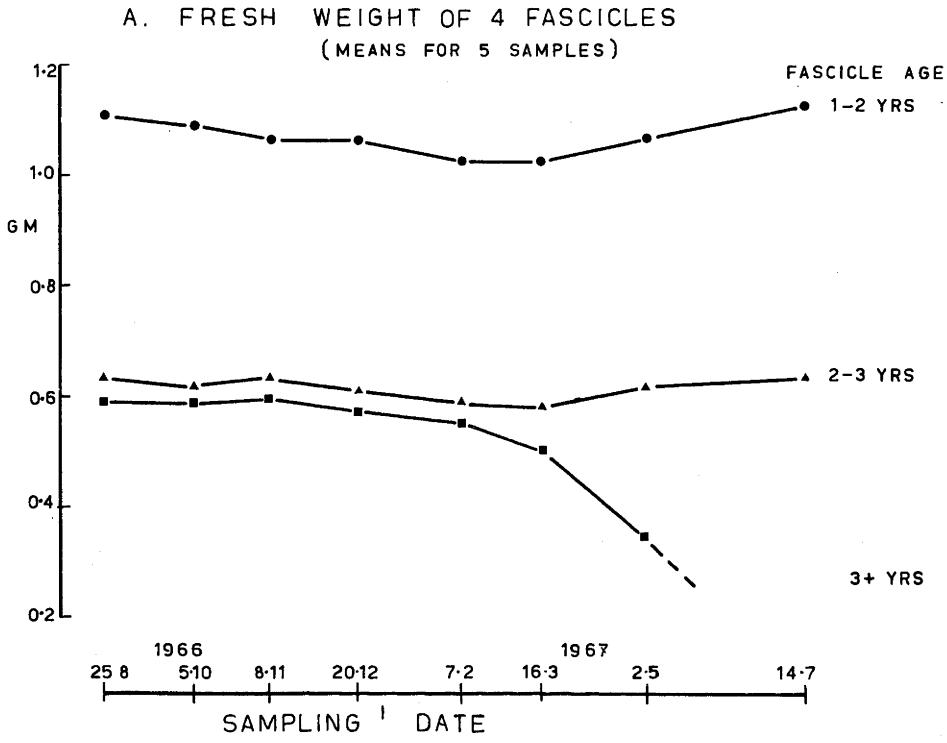
Leaves less than one year old were not studied because of the possibility that each collection might influence the development of remaining leaves. Wood (1968) observed P. radiata leaves can develop completely within the first year if conditions are favourable; while it is unlikely that the removal of a single mature fascicle from amongst several hundred at 6 - week intervals influences the structure and composition of the remaining leaves this might not be so during rapid shoot expansion.

3.2.2 Results and Discussion

Leaves from corresponding portions in adjacent trees vary greatly in weight; for example, the weight of four fascicles in the first collection ranged from 0.53 gm to 0.42 gm for 1 - year old leaves and 0.35 gm to 0.23 gm for 2 - years old leaves. Leaves of one age in different parts of the crown, or of successive ages at the same level also vary greatly in weight, presumably in response to both internal and external influences. Consequently, changes in leaf weights through the year and between years could not be satisfactorily studied by a simple analysis of variance. The calculation of successive leaf weights as a percentage of their initial weights, or analysis of covariance, could have been applied, but the data probably do not justify such treatment, particularly in view of the method of tree selection and the absence of other growth and environmental data. However, the mean leaf weights for the five trees illustrate closely the pattern of change through the year; as an example the dry weights of 1 - year old leaves are shown in Fig. 3.2 for all trees.

The fresh weights of P. radiata leaves varied only slightly during their second and third year on the branch (Fig. 3.1). The differences in weight between leaves initially 1 - and 2 - years old probably results from varying development during the first years growth of each,

FIG. 3-1 SEASONAL CHANGES IN THE COMPOSITION OF P. RADIATA FOLIAGE



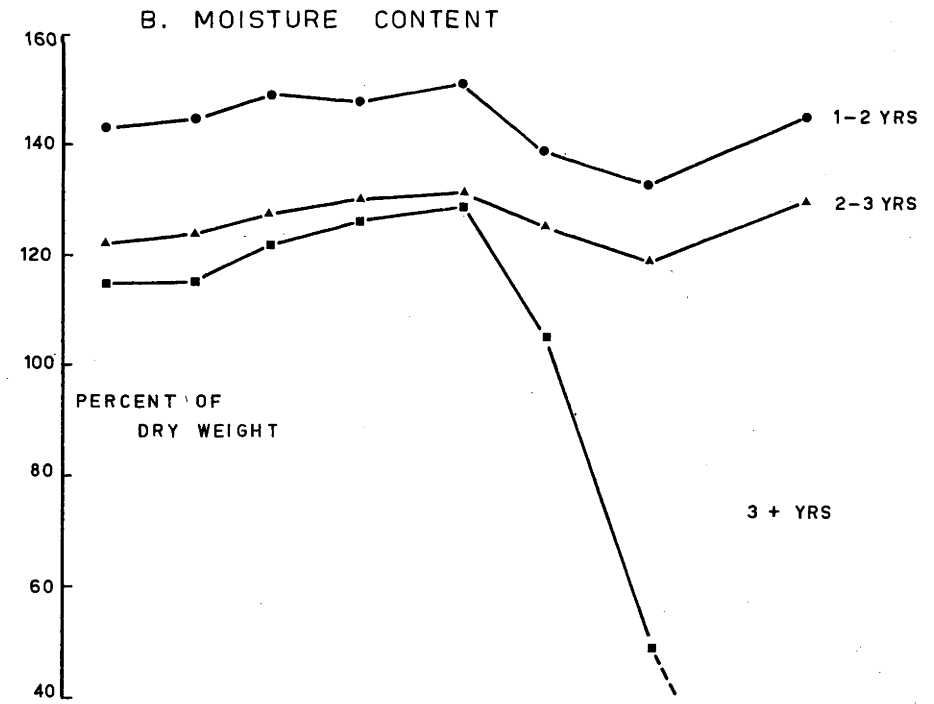
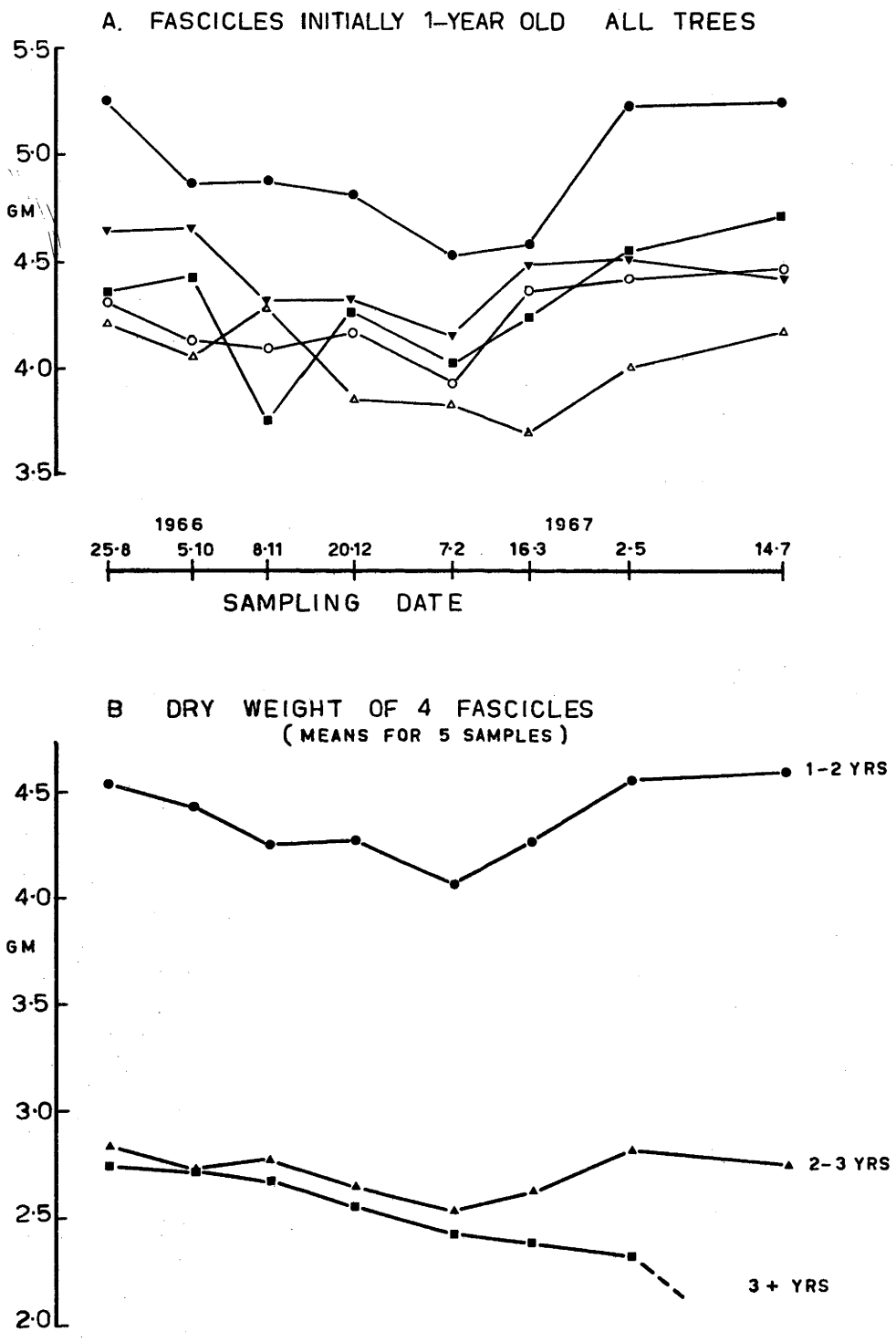


FIG. 3-2 SEASONAL CHANGES IN THE DRY WEIGHT OF P. RADIATA FOLIAGE



but whether the difference in development is due to physiological change with increasing tree age or to differing environmental conditions during the development of each was not ascertained. During the 12 - month study period the fresh weight of leaves initially 1 - and 2 -years old decreased slowly to a minimum during the late summer and then increased again to a value similar in each case to the initial value. The overall fluctuation for both ages was 9% of the average for the year.

The dry weights followed a similar trend through the year but the fluctuation was more marked than for fresh weights; overall fluctuation in dry weight was 12% of the years average. Tamm (1955) also observed greater fluctuation through the year in dry weights than fresh weights for both Pinus sylvestris and Picea abies although changes in both fresh and dry weights differed between years in both species. Although P. radiata may grow during all months of the year when temperature and soil moisture conditions are favourable annual growth is characterised by vigourous bole extension and lateral branch development during spring and early summer followed by a long period of slower growth which may be interrupted by bursts of growth or periods of near dormancy depending on environmental conditions (Fielding, 1955). Initially extension of new annual shoots probably involves utilization of carbohydrate photosynthates produced or stored elsewhere within the tree; later as leaves develop fully on the new shoots they become self supporting and make their contribution to overall tree growth.

The dry weights of leaves of all ages decreased during the spring and summer months (September - January) during the active growth period indicating a drain on photosynthates over their capacity to be supplied by current photosynthesis with those leaves. Later in the year, as total growth becomes less and the photosynthetic activity of newly

developed foliage increases, the dry weight of older leaves again increases till the weight at the beginning of the year is regained. Rutter (1957) and Kozlowski and Winget (1964) also concluded that reserves of carbohydrates within the tree may be essential to meet the requirements of new growth and for respiration at the beginning of each growing reason, but much of the new extension may be made from current photosynthesis in older leaves.

From 5 to 6 years of age P. radiata stands may increase in weight by 20 m tons per ha, but the foliage weight at the beginning of this period is only 2 m tons per ha. The present data indicates about 10% of the initial foliage weight may be used as reserve carbohydrate in new season extension, so reserves in leaves possibly contribute only 1% to total growth during the 5th year. Although not substantial in the total tree growth, this may still be of importance in ensuring rapid early development and hence a longer growing season. After canopy closure when leaf production has stabilized a 10% decrease in 3 - year old leaf weight due to recirculation of carbohydrates would provide much of the photosynthate necessary for early expansion but would amount to only 2% of the total annual increase.

Although the moisture content on a dry weight basis increases during the early part of the growing season and then decreases this is related to dry weight changes. The amount of water in the leaves (as the difference between fresh and dry weights) actually decreases steadily in early autumn and then increases to about the original level.

Leaves that were nearly 3 - years old at the beginning of the study year declined in a dry weight and water content as with the 2 - year old leaves. After mid - summer when the younger leaves began to regain weight, the dry weight of older leaves continued to decrease and their moisture content dropped sharply both in total amount and as percent of dry

weight. The older leaves along the branch turned brown and were progressively shed as each reached about 40 - 46 months age. Of the leaves regarded as 3 years old at the beginning of the growing season those nearest the bole began to fall during the late spring of that year and only a few produced late in the season remained at the end of the year.

3.2.3 Conclusions

The foliage of P. radiata trees at the beginning of a growing season is probably important for the production of photosynthates used in extending shoots; reserves of carbohydrates within the foliage may be important initially to ensure rapid early extension, but their total contribution to annual growth is small.

In the study area both the fresh and dry weights of leaves remained fairly constant after full development was reached, usually in the first year. During the fourth year the dry weight and water content decreased sharply for 3 - 4 months till the leaf died just before dropping off the branch. Older leaves lost nearly 20% of the dry weight of the previous winter before falling from the branch.

3.3 LITTER FALL IN P. RADIATA STANDS

3.3.1 Methods

Litter fall from the P. radiata trees was collected from two study plots over a period of 12 months from 22nd July, 1966 to 14th July, 1967. Leaves from young unpruned trees accumulate near the bole. Many standard types of litter frames are unsuitable for sampling close against the tree bole, and because of the variability in litter distribution many small litter frames would have been needed to obtain a reliable average litter value. One tree was selected at random from each of the five size classes (Chapter 2.2.5) in sample plots 1 and 4, in addition to the

two trees per class selected for dry weight estimates. Around each selected tree a frame 2.44 metres (8 ft) square with 15 cm (6 inch) high sides was constructed, using preservative treated calico as a base (Plates 2.1 and 2.3). Material which accumulated on each frame was collected at about six - week intervals.

3.3.2 Results and Discussion

The dry weights of litter falling in plot 1 (12 years old) and plot 4 (5 years old) during the twelve months from 20th June, 1966, are summarised in Table 3.1.

Within each plot the total amount of litter collected per frame through the year was closely related to the size of the tree surrounded by the frame. This result was expected for plot 4 where the trees are small and the older leaves are concentrated close to the bole on branches only a few feet above ground level. The distance leaves must fall from trees in plot 1 (5 - 15 metres) and the wider spread of leaves along the branches makes a relationship between leaf weight and tree size less likely. In fact, there is a more even distribution of litter beneath each tree than might be expected; 2.1 kg litter accumulated in the frame encircling the largest tree, only 27.5% greater than the amount in the frame encircling the smallest tree, while the largest tree (21 cm diameter) would normally shed about 4 kg leaves per annum and the smallest (10 cm diameter) would shed only 0.4 kg per annum (calculated from the total weights of foliage on the nine weighted sample trees). However this result indicates that where only a few collecting trays are used the result may be seriously biassed by chance location under particularly large or small trees, despite the even appearance of litter on the forest floor. The average dimensions of the five trees in each plot were close to the plot average and so the amount of litter collected is probably representative of the total

TABLE 3.1 Dry weight of litter falling in P. radiata stands of age series (kg per ha)

Collection	Study Plot 1 12 years		Study Plot 2 5 years	
	Leaves	Male cones	Leaves	Male cones
20- 7-66	---	collection frames located		---
25- 8-66	290	-	2	-
4-10-66	760	85	57	3.7
7-11-66	545	220	17	17.0
20-12-66	670	160	14	2.7
8- 2-67	335	3	14	-
16- 3-67	170	2	11	-
2- 5-67	200	-	28	-
17- 7-67	960	-	50	-
Total	3,930	470	194	23.4
Total litter fall ± S.E. (68%)		4,400 ± 265		217 ± 48
S.E. % (95%)		12.0		44.2

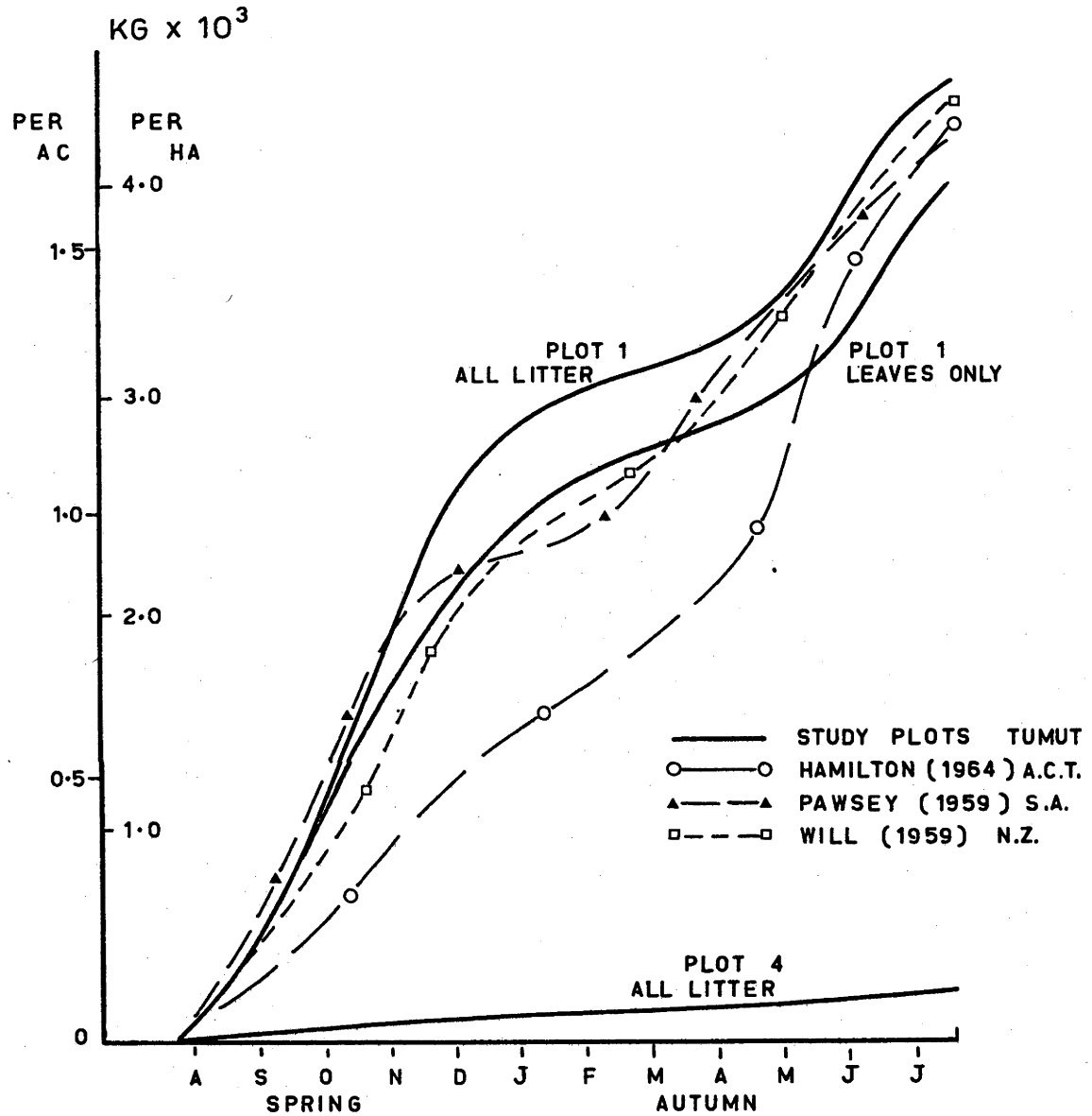
litter fall. The frames were made 2.44 m square to correspond with the theoretical tree spacing, however the actual spacing is slightly wider in both plots, so total weights of litter per unit area have been calculated from the proportion of the total plot area occupied by the litter frames.

During the twelve months of litter collection, total litter fall amounted to 4,400 kg per ha and 220 kg per ha in plots 1 and 4 respectively (age 12 and 5 years at the beginning of the study) and of this 8.4% in plot 1 and 10.8% in plot 4 was of male cone parts shed during and after pollen dispersal in early spring. In both plots nearly all the male cones produced had dried and been shed by the end of December (early Summer), thus turnover of this material is rapid but it represents only a small proportion of the total biomass.

Leaf shed was continuous throughout the year, but in both stands heavier than average falls occurred during October - December (late Autumn) and again during May - July (early winter). Records of litter fall from a range of situations (Fig. 3.3) show similar results. For all stands leaf fall was at a minimum during several mid - growing season months, but this varied from December - January (Pawsey, 1959) to February - March in the present study. The proportion of leaves shed before the summer decline varied considerably.

The similarity of total annual litter fall at the contrasting sites (Fig. 3.3) supports the conclusion that total leaf weight is relatively independent of site quality over a wide range of productive sites. Total leaf weight could be estimated for the two stands in the age series by assuming a 20% decrease in dry weight prior to shedding and also that 1 - and 2 - year old leaves were of comparable weight. By this method total leaf weight at age 5 and 12 years is estimated at 700 and 14,000 kg per ha respectively.

FIG. 3-3 ANNUAL LITTER FALL IN CLOSED CANOPY P.RADIATA PLANTATIONS



Leaf biomass estimated directly from sample trees (Chapter 2) was 2,000 and 10,000 kg per ha. In the younger plot an underestimate is expected because the weight of leaves developed on trees only 3 years old (i.e. the weight of 3 - year old leaves in plot 4) is substantially less than of leaves produced in the following years; but more similar values might have been expected for the 12 year old plot. The overestimate of foliage weight in the older plot probably results from the increased production of leaves as the tree canopy closed, but equally foliage production may have been less for physiological reasons in the 10th and 11th year than in the 9th year. Whatever the reason, collection of litter fall has not given a good estimate of stand foliage weight; records over a number of years and more detailed data on change in leaf weight with age are needed before this would be possible.

3.3.3 Conclusions

Litter fall from P. radiata stands is spread over the year but may be concentrated during autumn and early winter months. The amount and proportion of annual litter falling in any season varies between sites and probably between years depending on the environmental conditions which influence both the rate of new shoot and leaf development at the beginning of the cycle and the rate of drying and absicission at the end.

CHAPTER 4

CONCLUSIONS. ACCUMULATION AND TURNOVER OF ORGANIC MATTER IN PINE PLANTATIONS

CHAPTER 4

CONCLUSIONS. ACCUMULATION AND TURNOVER OF ORGANIC MATTER IN PINE PLANTATIONS

In the first few years, the young trees in a *P. radiata* plantation constitute only a small proportion of the total organic matter present. Commonly their growth is favoured by cutting back, either before or after the seedlings are planted, of other vegetation. Even with such treatment the weight of the pine trees in the study area did not exceed the weight of other organic matter until five years after planting.

The establishment spacing commonly used in plantations (2.5m x 2.5m) has been derived, from espacement experiments and accumulated field experience, as a suitable compromise between the effects of many factors including individual tree growth, growth per unit area, branch size, weed competition and minimum saleable bole size. At this spacing the crowns of individual trees expand rapidly for two or three years after the initial establishment period until a full canopy cover has been established; at the end of this time total foliage weight and photosynthetic capacity are at a maximum and so total production is also greater than at any other time.

After full canopy cover has been reached, the weight of foliage per unit area decreases initially as the mass of leaves produced immediately before canopy closure are shed, and then remains more or less constant as the area of crown surfaces exposed to light remains nearly constant. Total production also remains nearly constant for a number of years after canopy closure and consequently total bole wood production remains nearly constant, although average foliage efficiency

probably decreases slowly as green crown height, and consequently the energy necessary for water, mineral and photosynthate movement increases. The amount of respiration relative to photosynthesis is also important to total production, particularly after canopy closure (Hosner and Madgwick, 1967).

Foliage weight per unit area seems primarily dependent on the total surface area of all tree crowns which can be exposed to light intensities above a compensation point at which photosynthesis and respiration balance. The size, shape and weight of individual leaves may vary according to water and nutrient status, but within fairly wide extremes of site quality total foliage weight does not seem strongly related to site quality. Variation in production between contrasting sites is probably related closely to average photosynthetic efficiency during periods of metabolic activity, the seasonal duration of photosynthetic activity and leaf longevity, but few data are available from which the relative importance of these factors can be determined.

Total production is not always closely related to leaf weights through the age series (Table 4.1). Although leaf weight estimates may be imprecise, during the short period of maximum foliage and total dry weight production the net assimilation rate per unit leaf weight is greater than at any other time, even allowing for a later culmination of root production. Leaves older than one year contribute relatively more to total production before canopy closure than after (Table 4.1) and this would be expected since the proportion of older leaves in full sunlight is then greater.

After canopy closure the P. radiata plantation ecosystem is floristically and structurally simple. The amounts and distribution of organic matter within the ecosystem can be studied as a single unit comprised of canopy, bole, litter and root layers. The total canopy increases slowly as the amount of dead branch material below the live crown increases,

Table 4.1 Leaf weights and total production of *P. radiata* through the age series

Quantity of leaves ($kg/ha \times 10^3$)	Stand Age (years)				
	4	6	8	10	12
1 year old	0.57	2.55	3.88	3.21	3.29
2 years old	0.32	1.20	7.90	3.04	3.14
3 years old	0.15	0.57	2.55	3.88	3.21
Total	1.04	4.32	14.33	10.13	9.64
Total production in subsequent year ($kg/ha \times 10^3$)	3.7	32.9	22.0	20.0	20.0
Total production per unit leaf weight					
Production/ 1yr leaves	6.5	12.9	5.7	6.2	6.1
Production/ 2yr leaves	4.2	8.8	1.9	3.2	3.1
Production/ all leaves	3.6	7.6	1.5	2.0	2.1

although a substantial proportion of the total annual above-ground production (about 16% in the present study) is of foliage replacing older foliage in a three year turnover cycle. The production of bole and possible of root components is more or less constant after canopy closure until total production diminishes, but no data are available from the present study to quantify this decrease.

Turnover of the litter layers was rapid in the study area, with losses from decomposition at least balancing annual additions from litter fall after about 10 years, but the rate of litter breakdown is dependent on many external factors and so may vary substantially between sites.

The data collected of dry weight accumulation and distribution enable the calculation of nutrient element uptake and distribution through the age series, and in

addition provide a basis for an understanding of structural changes which occur in plantation stands under various site and management conditions. Some limitations to the study are evident and several areas can be defined where more intensive investigation is needed. These are:-

1. The present study was restricted to only above ground tree parts and the estimates of tree root weights are necessarily tentative. Furthermore, the weight of grasses and bracken fern below ground may be as great as above, but this has not been included in assessing changes in weight distribution.

2. The estimates of increment assume the five study plots are of an age series. All available data support this assumption and because of the large changes between plots, site variation would need to be great before the conclusions were invalidated. However, more intensive study is required to more closely define the changes in production with stand development. These studies should include (i) the photosynthetic capacity of leaves, and the variation with age of tree, age of leaves, position in tree and effect of shading, and (ii) the importance of respiration in woody tissues in relation to foliage net assimilation, and the influence of respiration on total production.

Results from these studies, together with the present data would allow more complete discussion of maximum and optimum production after canopy closure, the effects of thinning and pruning at varying intensities, the nature of crown expansion after thinning, and the transfer of production within dominance classes with stand age, all of which are important to the attainment of optimum bole wood production in maturing plantations.

3. In the present study the complete tree has been taken as the sample unit to increase the precision of stand nutrient content estimation, but this involved greater physical effort

than might be needed in other studies. Other sampling methods might be used if crown components and bole components were considered separately. The minor components cannot be accurately assessed on a whole tree basis. The statistical and economic advisability of regarding every component as a separate population and sampling each only to the intensity required needs to be considered.

PART II

ACCUMULATION, DISTRIBUTION AND TURNOVER OF MINERAL NUTRIENTS IN PLANTATIONS OF *PINUS RADIATA*

CHAPTER 5

DISTRIBUTION OF MINERAL NUTRIENTS IN *P. RADIATA* PLANTATIONS

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CHAPTER 5

DISTRIBUTION OF MINERAL NUTRIENTS IN P. RADIATA PLANTATIONS

5.1 INTRODUCTION

During recent years a number of studies have been made to determine the amounts of various nutrient elements contained within the trees or total ecosystem of forest stands.

Frequently concern has been expressed that continued harvesting of the tree crop might deplete the reserve of nutrients available from the soil, and some studies have been established mainly to asses the drain of nutrients incurred by logging, Will (1964, 1968) for instance concluded "soil nutrient reserves appear to be adequate to meet the demand in the immediate future" and "evidence is presented that cycling of nutrients in pumice soil under P. radiata plantations will retard serious depletion of nutrients for a second generation tree crop at least". Young, et al., (1965) and Young and Carpenter (1967) have prepared stand tables of chemical elements contained in trees of several species so the depletion of the mineral nutrient resource by harvesting can be estimated for any intensity of harvesting. Occasionally the amounts and distribution of mineral nutrients have been assessed so the growth of the tree crop and its response to mineral fertilizer addition could be more closely examined and related to the physiological processes involved (White, 1964; Madgwick, 1962). Other studies have attempted to relate the level of uptake and recirculation of nutrient elements within particular ecosystems to the requirements of an internally dynamic but structurally relatively stable plant community (Ovington, 1959c; Cole, et al., 1967).

These studies of forest ecosystems, together with more detailed studies of particular segments of the nutrient redistribution cycle, for example within the tree (Tamm, 1955), in litter fall and decomposition (Will, 1959; Miller and Hurst, 1957), in rainfall (Madgwick and Ovington, 1959; Attiwill, 1966b; Carlisle, et al., 1967) and in groundwater (Likens, et al., 1967) allow fairly complete and detailed evaluation of the total nutrient cycle for a number of forest stands. The pattern of mineral nutrient distribution and rate of turnover can probably be defined as well for plantations of P. radiata as for any tree species.

The evaluation of the total nutrient requirement of a tree stand is important to ensure high levels of production can be sustained within a single crop rotation and over successive rotations; consequently many "total tree" studies have been carried out within maturing stands. Studies of nutrient deficiency have usually been limited to long-term considerations, little attention being given to the manner in which the level of nutrients required to ensure maximum growth may vary as the forest stand matures.

The dry weights of five young P. radiata stands have been given previously, by combining this data with percentage nutrient content data the nutrient relationships of these stands can be examined.

5.2 LABORATORY PROCEDURES

5.2.1 The P. radiata trees

Nine trees were sampled from each of five study plots of the age series described in Chapter 2. The trees were subdivided into major components by age-strata and the dry weight of material in each unit determined; each unit was then carefully subsampled progressively until about 200 - 500 gms of a mixed representative sample remained. Foliage was subsampled by progressive quartering, branch

wood was broken into short lengths and then quartered to retain a correct proportion of thick and thin branches. Discs were taken regularly from the bole lengths so that the relative proportion of wood and bark could be ascertained (Chapter 2.2.5a), the bole bark was then sampled by quartering and the wood discs were quartered diametrically. Each sample was finely ground before storing in a small paper bag till required for analysis.

Prior to chemical analysis portions of each sample were redried at 85°C, and 0.5 - 1.0 gm was digested in a 1:4:15 mixture of sulphuric, perchloric and nitric acids (Piper, 1944). For foliage samples 0.5 gms proved adequate but for woody material 1.0 gms was required to give the correct range of cation concentrations in the digest solution.

The concentration of phosphorus in the digest solution was determined using a Beckman D.U.2 spectrophotometer after the yellow colour of the molybdo - vanadate complex was formed (Piper, 1944). Manganese and zinc concentrations were determined directly from the digest solution using a Techtron atomic absorption spectrophotometer. For potassium, magnesium and calcium equal quantities of digest solution and 5% lanthanum chloride solution were taken and made up to a final volume appropriate to the cation concentration, and the three cations were determined using the Techtron spectrophotometer.

The cation analysis techniques followed closely the principles established by Willis (1960, 1963). Ionic interference occurred in the measurement of both calcium and magnesium absorption due to the frequent high concentrations of these cations and other ions such as phosphorus and aluminium. Lanthanum chloride added at a concentration of 1% in the final solution was used to supress interference (Willis, 1960).

Samples were taken for analysis at random in batches of 20 - 40 to make best use of the equipment and time available. About 10% of samples in each batch were repeated in later batches, and samples showing substantial discrepancy from other results were also repeated. This duplication indicated a reproducability within ± 5% for all elements reported.

The significance of subdivision in the tree by vertical age-strata should be noted. For each major component all material contained in the uppermost 1965 - 1966 growth zone was produced only during that growing season. Material in the next (lower) 1964 - 1965 growth zone was initiated in 1964 - 1965 and extended during 1965 - 1966; and so on down the tree. Consequently while the foliage sample for 1965 - 1966 contains only leaves of that year's growth the successively lower (1964 - 1965, 1963 - 1964,--------etc) samples contain a composite of two, three, -----etc, years growth. The proportion that each year's growth contributes to the total of age-strata below 1965 - 1966 varies considerably between trees, even between trees of comparable size and total weight characteristics. Stem leaf growth is unique in that one-years growth is present on each of the bole age-strata.

5.2.2 The associated vegetation and litter layers

The collection of other living vegetation and the organic matter of the litter layers from twenty 1/16 square metre quadrats per study plot has been described (Chapter 2). After oven drying a sub-sample of each sample was obtained by progressive quartering. The sub-sample was ground to a fine powder prior to analysis for the six mineral elements as described previously. The weights of nutrients on an area basis were calculated by combining nutrient concentrations and dry weight data.

Sampling errors present in the estimation of each vegetation and litter category are large because of the small number of samples in which each category was recorded. Confidence limits have been calculated for the total of each nutrient in the combined vegetation and litter layers.

5.3 RESULTS AND DISCUSSION. NUTRIENT CONTENT OF THE *P. RADIATA* TREES

5.3.1 Nutrient concentrations within sample trees

The concentrations of the nutrient elements determined are summarised in Tables 5.1 a - 5.1 f, the values reported being averages for nine trees in each study plot. Although there is considerable between-tree variation in nutrient concentrations for comparable samples (c.f. Chapter 5.3.2), the results indicate the general trends in nutrient distribution.

The magnitude and significance of between-plot variation is considered more fully in Chapter 5.3.3, but there is little evidence of marked variation in nutrient concentrations for comparable material between the five study plots. Consequently the general trends in nutrient concentration are discussed with reference mainly to the oldest plot, No. 1, age 12 years (Figs. 5.1 a - 5.1 f).

Nutrients are usually most concentrated in the foliage and decrease progressive in the bole bark, branch wood and bole wood, as reported by Metz and Wells (1965) and Xydias (1964). Most nutrients are involved directly in the metabolic processes of living cells, particularly the meristematic cells, and consequently their concentration is greatest in zones of active growth and decreases as the proportion of non-living material in the sample increases. In the sample trees, leaves along the bole consistently had higher levels of all nutrients than leaves of a comparable age on lateral branches, and the concentration of nutrients in female cones was usually intermediate between branch wood and bole wood.

FIG. 5-1 THE CONCENTRATIONS OF MINERAL NUTRIENTS IN COMPONENTS OF TWELVE YEAR OLD P.RADIATA TREES

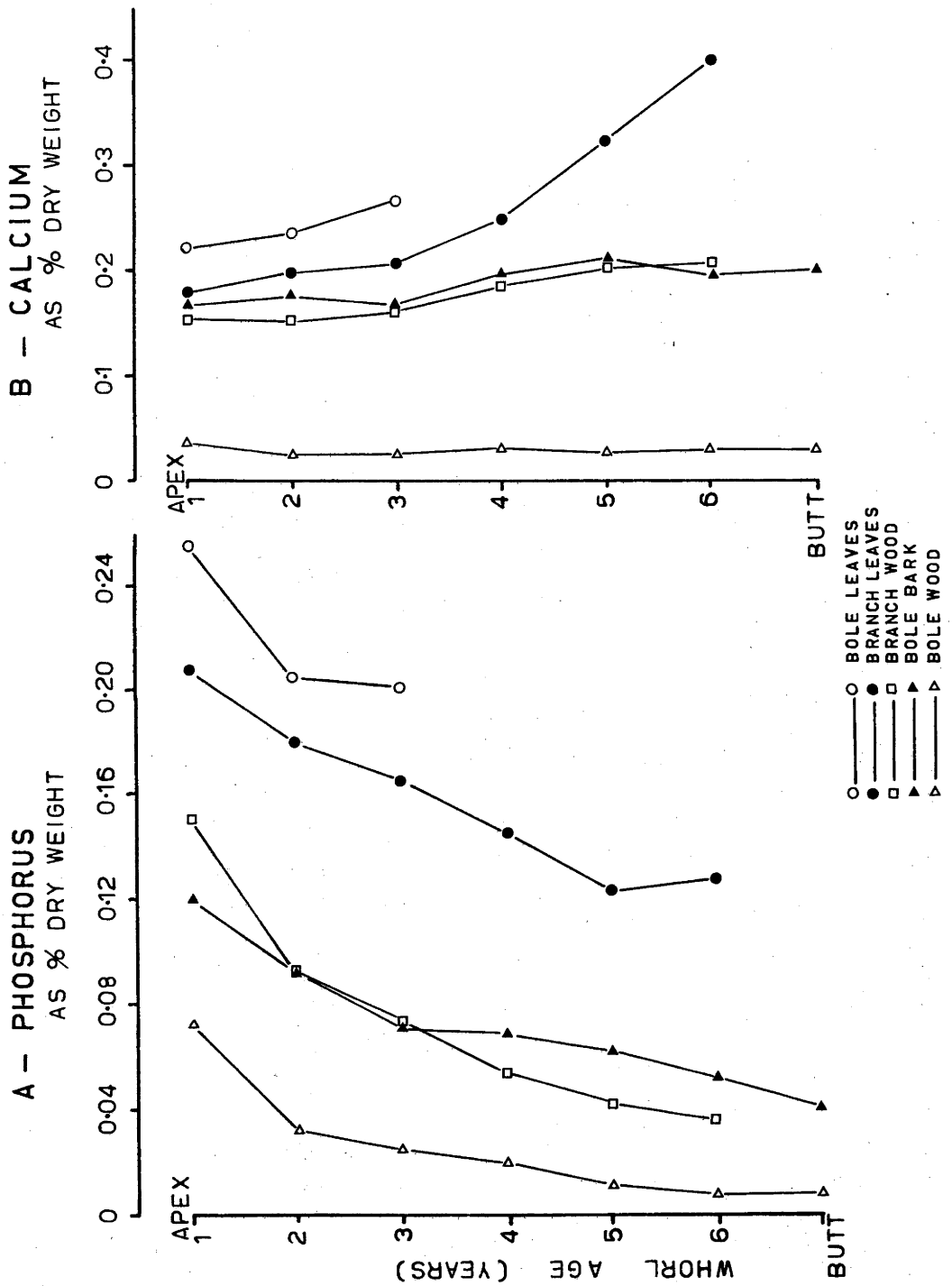


FIG. 5-1 THE CONCENTRATIONS OF MINERAL NUTRIENTS IN COMPONENTS OF 12-YEAR OLD P. RADIATA TREES

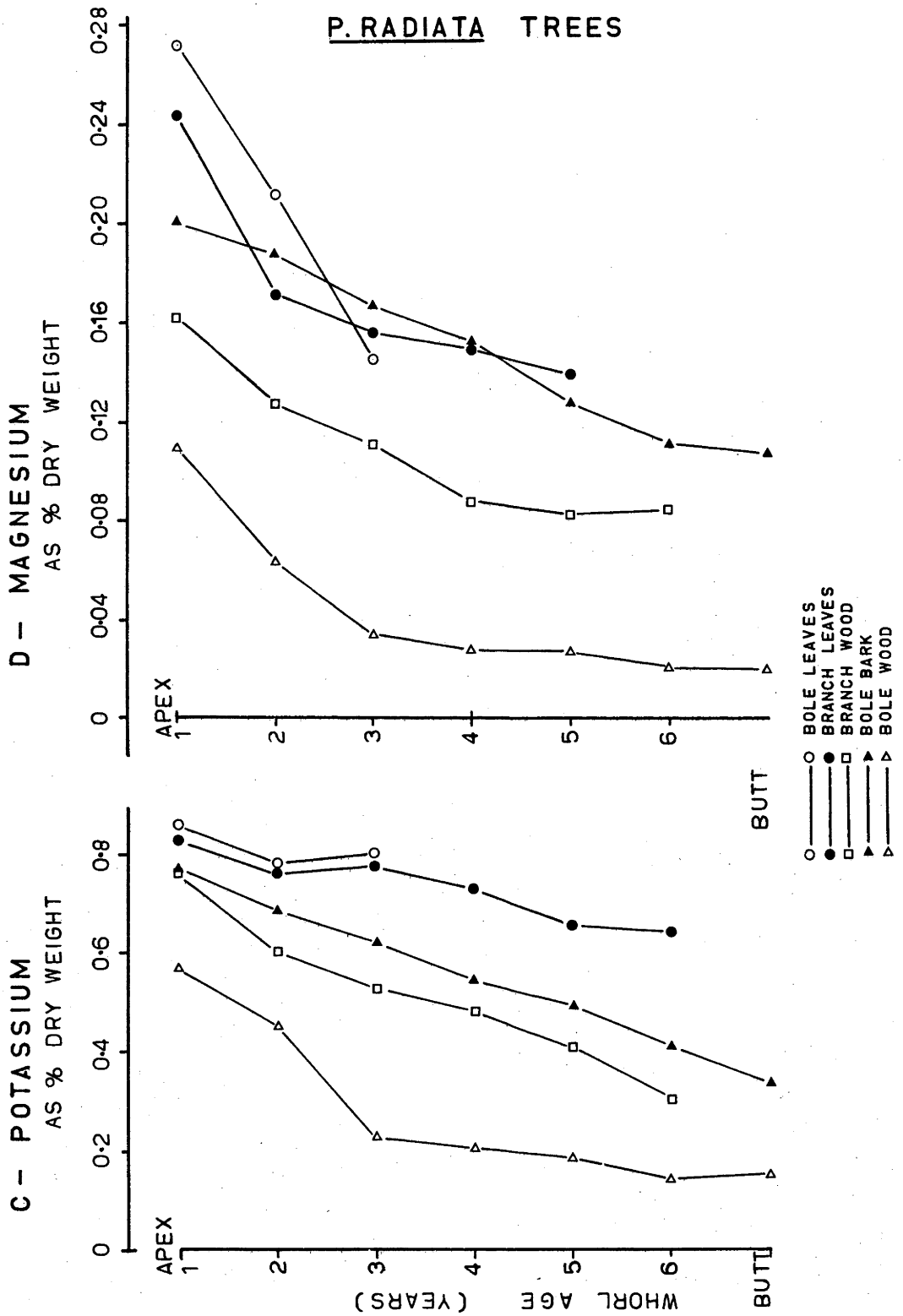
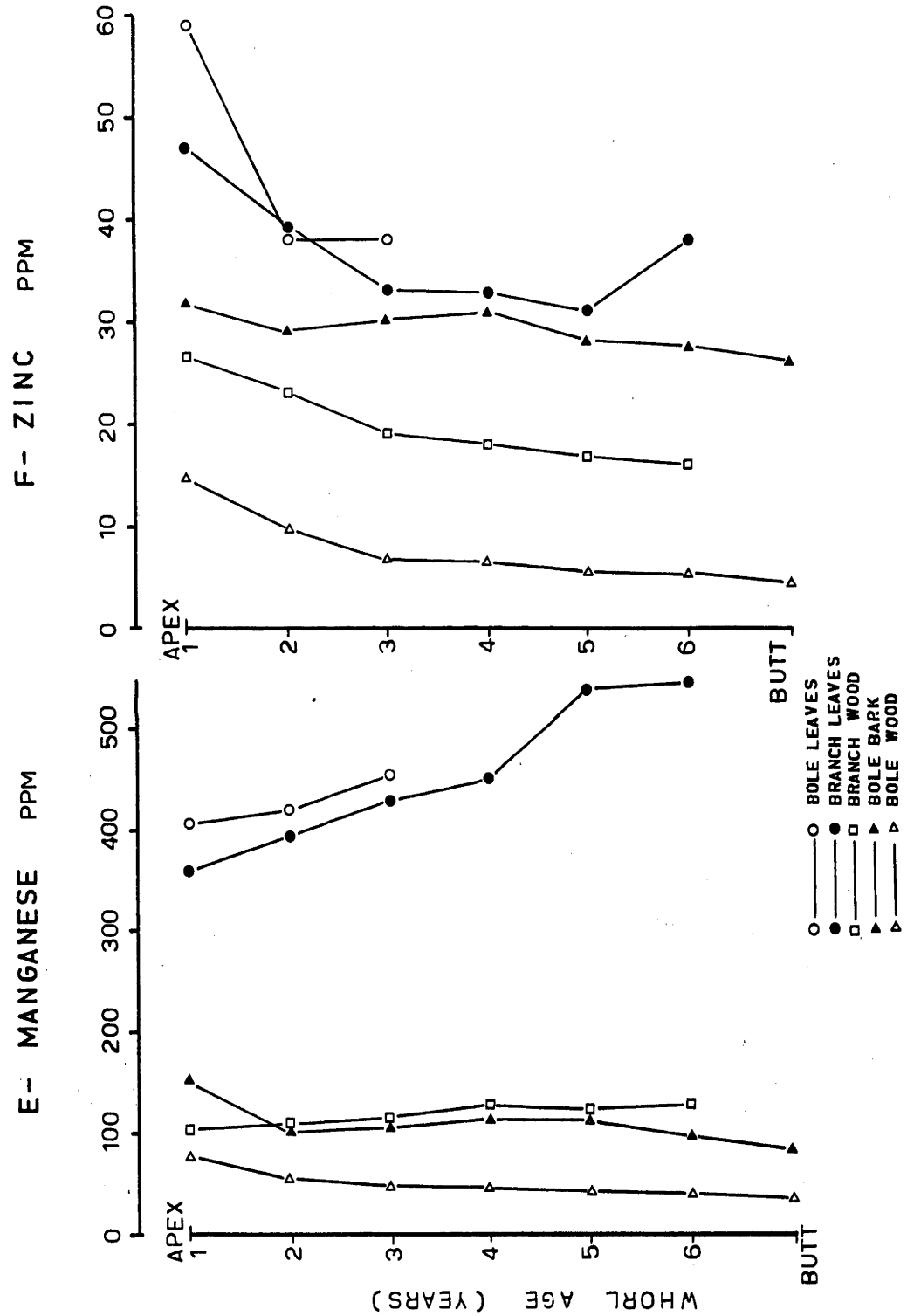


FIG. 5-1 CONCENTRATIONS OF MINERAL NUTRIENTS IN COMPONENTS OF 12-YEAR OLD P. RADIATA TREES



Nutrient concentration changes due to age of component, position within the tree, site, season, etc., have been reported in many studies (e.g. White, 1954; Tamm, 1955; Will, 1957; Humphreys and Kelly, 1962; Wells and Metz, 1963; Lowry and Avard, 1965; Miller, 1966), and the effects of such differences in sampling for chemical analysis have been briefly reviewed for P. radiata (Raupach, 1967a). The nutrient values determined for the sample trees of each study plot (Table 5.1 a - f) are generally of the same order of magnitude as have been reported elsewhere for radiata pine (e.g. Will, 1957; Orman and Will, 1960; Humphreys and Gentle, 1968) and for other species (e.g. Ovington, 1956; Beaton, et al., 1965; Beaton, et al., 1965; Guha and Mitchel, 1965, 1966; Bazilevič and Rodin, 1966) although some appreciable differences do occur and will be described later.

Typical reported levels of nutrient element concentration are presented for comparison with the present results in Table 5.2. A wide range of coniferous species and localities are represented; the results of Orman and Will (1960) and Will (1964) for P. radiata in New Zealand are the most suitable for comparison because of completeness and similarity of site.

For most components the nutrients present decreased in the order potassium > calcium > magnesium > phosphorus > manganese > zinc. The concentrations of phosphorus, potassium, magnesium and zinc decreased within all components with increasing distance from the apex of the tree (i.e. with increasing average age), while for calcium there is an increase with age for all components except bole wood where calcium concentration was relatively constant. Manganese concentrations decreased slightly with average age through the bole wood and bark, but increased with age in the canopy components, particularly the foliage.

TABLE 5.1 a Concentration of phosphorus in sample trees of *P. radiata* age series

(Average values as percent dry weight for 9 trees per plot)

Component	Age-strata	Study Plot Number / Age				
		5	4	3	2	1
		3 yrs	5 yrs	7 yrs	9 yrs	12 yrs
Branch wood	1965-66	0.120	0.126	0.189	0.153	0.151
	1964-65	0.094	0.081	0.086	0.079	0.092
	1963-64	0.082	0.054	0.056	0.044	0.074
	1962-63		0.045	0.040	0.028	0.054
	1961-62			0.041	0.028	0.042
	1960-61					0.036
Branch leaves	1965-66	0.171	0.179	0.237	0.186	0.208
	1964-65	0.148	0.136	0.163	0.148	0.180
	1963-64	0.141	0.125	0.129	0.117	0.166
	1962-63		0.110	0.109	0.094	0.146
	1961-62			0.102	0.091	0.123
	1960-61					0.128
Stem leaves	1965-66	0.173	0.172	0.290	0.202	0.256
	1964-65	0.142	0.131	0.206	0.161	0.206
	1963-64	0.125	0.134	0.154	0.115	0.203
Bole bark	1965-66	0.116	0.118	0.144	0.124	0.122
	1964-65	0.102	0.092	0.101	0.086	0.092
	1963-64	0.083	0.078	0.076	0.069	0.074
	1962-63		0.075	0.061	0.060	0.069
	1961-62			0.046	0.051	0.062
	1960-61			0.050	0.036	0.052
	Butt					0.041
Bole wood	1965-66	0.061	0.046	0.063	0.044	0.072
	1964-65	0.038	0.022	0.022	0.019	0.032
	1963-64	0.023	0.016	0.013	0.013	0.026
	1962-63		0.011	0.011	0.088	0.019
	1961-62			0.007	0.004	0.011
	1960-61			0.007	0.004	0.008
	Butt					0.006
Cones				0.121	0.123	0.067

TABLE 5.1 b Concentration of calcium in sample trees of *P. radiata* age series

(Average values as percent dry weight for 9 trees per plot)

Component	Age-strata	Study Plot Number / Age				
		5	4	3	2	1
		3 yrs	5 yrs	7 yrs	9 yrs	12 yrs
Branch wood	1965-66	0.101	0.099	0.096	0.108	0.153
	1964-65	0.118	0.115	0.119	0.117	0.150
	1963-64	0.139	0.120	0.132	0.129	0.161
	1962-63		0.156	0.168	0.146	0.183
	1961-62			0.181	0.178	0.201
	1960-61					0.206
Branch leaves	1965-66	0.165	0.149	0.174	0.171	0.176
	1964-65	0.192	0.214	0.237	0.175	0.197
	1963-64	0.268	0.267	0.314	0.197	0.206
	1962-63		0.350	0.388	0.238	0.249
	1961-62			0.453	0.290	0.322
	1960-61					0.399
Stem leaves	1965-66	0.192	0.187	0.213	0.194	0.222
	1964-65	0.297	0.293	0.249	0.166	0.234
	1963-64	0.359	0.386	0.320	0.205	0.260
Bole bark	1965-66	0.204	0.149	0.144	0.132	0.172
	1964-65	0.167	0.172	0.161	0.132	0.174
	1963-64	0.171	0 183	0.183	0.144	0.168
	1962-63		0.180	0.200	0.145	0.194
	1961-62			0.192	0.142	0.208
	1960-61				0.141	0.196
	Butt					0.198
Bole wood	1965-66	0.067	0.034	0.026	0.029	0.036
	1964-65	0.043	0.030	0.028	0.031	0.028
	1963-64	0.031	0.031	0.030	0.036	0.028
	1962-63		0.029	0.032	0.032	0.030
	1961-62			0.030	0.030	0.027
	1960-61				0.029	0.028
	Butt					0.029
Cones				0.024	0.031	0.026

TABLE 5.1 c Concentration of potassium in sample trees of *P. radiata* age series

(Average values as percent dry weight for 9 trees per plot)

Component	Age-strata	Study Plot Number / Age				
		5	4	3	2	1
		3 yrs	5 yrs	7 yrs	9 yrs	12 yrs
Branch wood	1965-66	0.874	0.801	1.021	1.049	0.769
	1964-65	0.741	0.579	0.697	0.691	0.600
	1963-64	0.672	0.487	0.401	0.488	0.534
	1962-63		0.438	0.326	0.409	0.482
	1961-62			0.306	0.309	0.412
	1960-61					0.306
Branch leaves	1965-66	0.924	0.909	1.087	1.000	0.838
	1964-65	0.840	0.743	0.844	0.909	0.771
	1963-64	0.746	0.582	0.643	0.780	0.781
	1962-63		0.560	0.552	0.647	0.730
	1961-62			0.503	0.583	0.660
	1960-61					0.652
Stem leaves	1965-66	0.894	0.901	1.255	1.158	0.860
	1964-65	0.750	0.669	0.919	0.892	0.782
	1963-64	0.678	0.727	0.785	0.940	0.806
Bole bark	1965-66	0.816	0.801	1.104	0.991	0.771
	1964-65	0.647	0.583	0.877	0.820	0.693
	1963-64	0.516	0.471	0.698	0.669	0.622
	1962-63		0.449	0.546	0.634	0.557
	1961-62			0.388	0.546	0.498
	1960-61				0.434	0.414
	Butt					0.342
Bole wood	1965-66	0.587	0.408	0.769	0.816	0.579
	1964-65	0.394	0.241	0.302	0.524	0.459
	1963-64	0.240	0.213	0.223	0.380	0.228
	1962-63		0.169	0.179	0.234	0.202
	1961-62			0.107	0.169	0.182
	1960-61				0.131	0.146
	Butt					0.172
Cones				0.420	0.408	0.248

TABLE 5.1 d Concentration of magnesium in sample trees of *P. radiata* age series

(Average values as percent dry weight for 9 trees per plot)

Component	Age-strata	Study Plot Number / Age				
		5	4	3	2	1
		3 yrs	5 yrs	7 yrs	9 yrs	12 yrs
Branch wood	1965-66	0.114	0.097	0.129	0.137	0.161
	1964-65	0.122	0.098	0.105	0.108	0.128
	1963-64	0.134	0.111	0.099	0.101	0.111
	1962-63		0.124	0.118	0.096	0.088
	1961-62			0.119	0.089	0.083
	1960-61					0.085
Branch leaves	1965-66	0.119	0.126	0.176	0.176	0.245
	1964-65	0.114	0.122	0.132	0.130	0.171
	1963-64	0.118	0.115	0.135	0.118	0.158
	1962-63		0.127	0.160	0.124	0.150
	1961-62			0.178	0.142	0.141
	1960-61					0.152
Stem leaves	1965-66	0.128	0.123	0.184	0.263	0.270
	1964-65	0.102	0.096	0.103	0.136	0.146
	1963-64	0.122	0.107	0.096	0.070	0.132
Bole bark	1965-66	0.122	0.113	0.133	0.196	0.207
	1964-65	0.109	0.114	0.118	0.148	0.188
	1963-64	0.113	0.121	0.118	0.136	0.169
	1962-63		0.129	0.126	0.125	0.153
	1961-62			0.101	0.108	0.128
	1960-61				0.098	0.113
	Butt					0.108
Bole wood	1965-66	0.086	0.053	0.071	0.088	0.110
	1964-65	0.045	0.033	0.036	0.056	0.064
	1963-64	0.033	0.029	0.029	0.035	0.034
	1962-63		0.028	0.029	0.029	0.029
	1961-62			0.022	0.024	0.027
	1960-61				0.025	0.022
	Butt					0.021
Cones				0.104	0.109	0.075

TABLE 5.1 e Concentration of manganese in sample trees of *P. radiata* age series

(Average values as parts per million for 9 trees per plot)

Component	Age-strata	Study Plot Number / Age				
		5	4	3	2	1
		3 yrs	5 yrs	7 yrs	9 yrs	12 yrs
Branch wood	1965-66	118	99	74	117	103
	1964-65	151	135	91	128	109
	1963-64	172	176	111	151	113
	1962-63		192	130	166	128
	1961-62			128	184	124
	1960-61					129
Branch leaves	1965-66	251	254	301	343	361
	1964-65	295	321	357	350	397
	1963-64	394	394	435	380	430
	1962-63		474	482	420	452
	1961-62			512	463	544
	1960-61					546
Stem leaves	1965-66	280	290	294	370	409
	1964-65	386	389	346	322	421
	1963-64	427	485	399	400	458
Bole bark	1965-66	141	73	58	104	153
	1964-65	136	120	70	104	104
	1963-64	145	123	75	109	113
	1962-63		115	83	125	111
	1961-62			70	127	98
	1960-61				106	86
	Butt					49
Bole wood	1965-66	100	59	27	46	78
	1964-65	77	51	28	45	58
	1963-64	59	44	31	51	48
	1962-63		42	40	53	47
	1961-62			35	51	42
	1960-61				41	41
	Butt					35
Cones				25	20	17

TABLE 5.1 f Concentration of zinc in sample trees of *P. radiata* age series

(Average values as parts per million for 9 trees per plot)

Component	Age-strata	Study Plot Number / Age				
		5	4	3	2	1
		3 yrs	5 yrs	7 yrs	9 yrs	12 yrs
Branch wood	1965-66	44	30	26	26	27
	1964-65	58	41	21	18	23
	1963-64	64	49	20	18	19
	1962-63		59	19	18	18
	1961-62			18	16	17
	1960-61					16
Branch leaves	1965-66	51	39	43	40	47
	1964-65	55	40	33	27	39
	1963-64	60	48	27	22	33
	1962-63		62	29	23	33
	1961-62			30	23	32
	1960-61					38
Stem leaves	1965-66	53	39	48	50	60
	1964-65	56	43	30	31	39
	1963-64	61	58	23	20	38
Bole bark	1965-66	55	30	23	27	32
	1964-65	53	39	23	22	29
	1963-64	55	40	24	23	30
	1962-63		42	24	23	31
	1961-62			23	23	28
	1960-61				18	28
	Butt					26
Bole wood	1965-66	23	18	10	14	15
	1964-65	17	15	8	9	10
	1963-64	14	13	6	8	7
	1962-63		11	6	6	7
	1961-62			5	5	6
	1960-61				5	5
	Butt					4
Cones				10	9	7

A brief examination of the concentration of each nutrient determined follows because of the application in later discussion to rate of nutrient uptake.

(i) Phosphorus

The concentrations of phosphorus in the foliage of sample trees were similar to those reported for healthy P. radiata from a wide range of sites (Table 5.2). The concentrations in the current years foliage are greater for all trees than the 0.14% dry weight suggested by Raupach (1967b) as the level at which phosphorus may become limiting.

Average concentrations of phosphorus in other components are greater than reported for P. radiata in New Zealand, possibly because of differences in tree age and development. For example, average phosphorus values in the bole wood ranged from 0.08% at the apex to 0.008% dry weight at the base, while the overall average for the New Zealand trees was 0.007%. The New Zealand trees were 40 cm diameter and a vary sharp decline in phosphorus occurred from the outer sapwood to the heartwood (0.01% to 0.003%).

Nutrient differences between young, actively growing woody tissue and older wood have been reported and have been considered to show a withdrawal of nutrients from the heartwood (Beadle and White, 1968). The decrease in average phosphorus concentration in the bole wood from the apex to the butt zone in this study, and the marked gradient across the sapwood and into the heartwood reported by Orman and Will (1960) suggests that if nutrient withdrawal is involved it would be of considerable importance in the overall nutrient balance of P. radiata.

(ii) Calcium

Calcium concentrations within the study trees are very similar to those of the New Zealand trees for all components. Calcium concentration usually increases with tissue age, particularly in branch leaves, but no marked change occurred

TABLE 5.2 Typical values reported for concentrations of nutrient elements in conifer forests

Source	Details of Sample	Concentration (Range or Average) P(%)	Ca(%)	K(%)	Mg(%)	Mn(ppm)	Zn(ppm)
1. P. radiata,	all foliage, 4 trees	0.11-0.28	0.04-0.65	0.65-1.08	0.07-0.32		
2. P. radiata,	current foliage, 14 sites.	0.06-0.31	0.07-0.39	0.59-1.15	0.07-0.89	20- 502	21-120
3. 2 pines,	3 sites, foliage	0.07-0.13	0.47-0.95	0.38-0.56	0.09-0.12	400-2,500	
10 conifers,	3 sites foliage	0.08-0.21	0.38-1.37	0.30-0.50	0.09-0.19	500-9,900	
4. P. contorta,	5 sites foliage	0.08-0.18	0.16-0.64	0.32-0.62	0.09-0.14		
7 conifers,	25 sites, foliage	0.11-0.29	0.16-1.16	0.28-1.20	0.06-0.18		
5. P. contorta,	12 trees foliage					290- 410	44- 52
Douglas Fir,	4 sites, foliage					450-1,150	16- 36
Western Hemlock,	2 sites foliage					1,580-1,980	3- 12
6. P. radiata, (26-29yrs. old)	8 trees, foliage	0.18	0.12	0.90			
	branches	0.018	0.15	0.20			
	bark	0.10-0.007	0.08-0.94	1.00-0.03			
	wood	0.003-0.01	0.02-0.04	0.04-0.09			
7. P. radiata, (12yrs. old)	24 trees, foliage	0.15	0.33	0.99	0.12		
	branches	0.03	0.19	0.27	0.07		
	boles	0.01	0.08	0.12	0.04		

(continued on next page)

TABLE 5.2 (continued)

Source	Details of Sample	Concentration (Range or Average) P(%)	Ca(%)	K(%)	Mg(%)	Mn(ppm)	Zn(ppm)
8. P.radiata, (Present study. Plot 1 12yrs,old)	9 trees, foliage	0.12-0.21	0.18-0.45	0.55-0.84	0.14-0.25	360- 620	32- 51
	branches	0.03-0.15	0.15-0.23	0.20-0.77	0.08-0.16	103-142	16- 27
	bole bark	0.03-0.12	0.17-0.21	0.24-0.77	0.05-0.21	50-153	24- 32
	bole wood	0.008-0.07	0.03-0.04	0.15-0.58	0.02-0.11	35- 78	5- 15

References:

1. Will, 1957.
2. Humphreys and Gentle, 1968.
3. Ovington, 1956.
4. Beaton, Moss, et al., 1965.
5. Beaton, Brown, et al., 1965.
6. Orman and Will, 1960.
7. Will, 1964.
8. Present study.

in calcium concentration with height in the bole wood. Orman and Will (1960) reported only a relatively small increase in concentration across the bole towards the heartwood.

(iii) Potassium

Potassium occurs in the greatest concentration of all the mineral elements analysed in the study trees. Potassium concentrations in the foliage (0.5 - 1.1% dry weight) are slightly less than the average (0.9%) reported by Will (1964) and Orman and Will (1960), but the concentrations for all other components are greater in the Tumut sample trees.

The greater concentration for the Tumut trees may result partly from the younger age of the sample trees (as for phosphorus), but Will (1964) reported low concentrations (0.12%) for the bole wood of equally young radiata pine. On a site deficient in potassium, young radiata pine contained 0.05% in the boles of untreated trees and 0.09% in treated trees several years after potassium fertilization (Hall and Raupach, 1963; F. McKinnel, pers. comm.). The butt sections of larger trees in plot 1 have an average potassium concentration of 0.15% in the bole wood at the base, and the values are much greater (0.5%) in the tops of those trees. The average potassium concentration is similar in the bole wood of trees of plots 2 and 3 (0.14% in the butt zone), but is greater in younger trees (0.19% and 0.23% in the butt zone of plots 4 and 5 respectively) where very young tissue is more abundant. Consequently the average potassium concentration in the butts of trees in the study area will possibly decrease as heartwood formation increases.

(iv) Magnesium

The concentrations of magnesium in the various components of the sample trees are slightly greater than the averages reported by Will (1964). Magnesium concentration decreases down the tree for all components, the decrease being more marked than observed by Will (1957), although the

patterns of distribution are frequently less clear for magnesium than for other nutrients.

(v) Manganese

Fewer data are available in the literature for minor nutrients such as manganese and zinc in forest trees, despite evidence of the limitations of tree growth caused by soil deficiencies for these elements; for example, zinc deficiency in commercial plantations of radiata pine in Australia was reported in 1938 (Hearman, 1938). The paucity of data probably results in part from difficulties in assessing quantitatively minor nutrients, particularly under conditions of deficiency. The situation is improving with the development of spectrochemical techniques (e.g. Guha and Michell, 1965) but currently data are limited.

The concentration of manganese in 1 - year old leaves of the sample trees is within the range generally reported for P. radiata, although on poorer sites manganese levels are often very much less (Humphreys and Gentle, 1968). The concentration of manganese is commonly very much less in P. radiata than in many other coniferous species (Table 5.2), although this may only reflect a lower manganese availability in some Australian soils. Manganese is most concentrated in the foliage of the Tumut trees, young leaves usually contain more than 300 ppm, and the average concentration increases with leaf age. The foliar concentrations of manganese are about double those of other components; a very slight increase in manganese concentration occurs in the branch wood down the tree, but manganese decreases down from the apex in both bole bark and wood, with very low levels (85 ppm and 35 ppm respectively) at the base.

(vi) Zinc

Zinc occurs at lesser concentrations in all components than the other nutrient elements determined; values over 100 ppm were rarely recorded.

Levels in 1 - year old foliage (40 - 50 ppm) are similar to other results (Table 5.2), but zinc concentrations in older leaves are variable (see Chapter 5.3.3). There is a decrease in zinc concentration down the tree for all other components as the average age of the tissue increases. Zinc concentrations decrease to very small values (5 ppm) particularly in the bole wood, although the rate of decrease is less than for some other elements such as potassium and phosphorus.

Summary

The nutrient distribution patterns through the sample trees of each study plot illustrate concentration changes with age of tissue, between components and with varying proportions of active cells in the component samples. These distribution patterns and the levels of nutrients present are similar to the results reported for other studies of P. radiata and of other species. Some factors which may contribute to the apparent change in nutrient concentration with tissue age are discussed in Chapter 6.

5.3.2 Comparison of nutrient concentration between sample trees

In addition to variation in the concentrations of nutrient elements within individual tree crowns and boles with age, position, etc. variation from tree to tree within a stand has been widely reported. Assessments of within-stand variation in nutrient concentration have been done to facilitate subsequent sampling for diagnostic purposes (Lowry and Avard, 1965; Metz, et al., 1966), but generally such variation has received little critical examination.

The relationships between nutrient concentrations in branch leaves of the uppermost (1965 - 66) age strata and tree diameter are listed in Table 5.3 for the five study

TABLE 5.3 Correlation coefficients between nutrient concentration in 1 - year old foliage and tree diameter in P. radiata age series

Nutrient Element	Study Plot Number / Age				
	1 / 12	2 / 9	3 / 7	4 / 5	5 / 3
Phosphorus	-0.04	-0.05	0.61 -o-	0.53	-0.22
Calcium	0.10	-0.66 -o-	0.24	-0.44	-0.06
Potassium	0.55	0.26	0.12	0.52	-0.18
Magnesium	-0.73*	-0.01	0.08	-0.66 -o-	-0.55
Manganese	-0.47	-0.22	0.42	-0.38	-0.38
Zinc	0.26	0.54	0.35	-0.45	0.15

-o- Significant at P = 0.10

* Significant at P = 0.05

** Significant at P = 0.01

plots of the age series. Only for magnesium in plot 1 is there a significant relationship between concentration and tree size ($P = 0.05$), although at $P = 0.10$ relationships are significant for phosphorus in plot 3, calcium in plot 2, and magnesium in plots 1 and 4. For no nutrient is there a marked and consistent trend towards either a positive or negative relationship with tree size, except perhaps for magnesium where in three of the plots a negative relationship is indicated. The distribution of magnesium within and between trees is discussed again in Chapter 5.3.3.

When each plot is considered separately, foliar nutrient concentrations appear to be unrelated to tree size except possibly in plot 4 where trends towards negative correlations between size and the concentrations of calcium, magnesium, manganese and zinc, and positive correlations with phosphorus and potassium concentration are indicated. Shibamoto and Tajima (1961) reported nitrogen and phosphorus levels in the current foliage of Chamaecyparis to be directly related to tree height and calcium concentration to be inversely related to tree height, and similar results were reported for larch (Leyton, 1956) and for Scots pine (Leyton and Armson, 1955) when leaves from terminal shoots were analysed. Ovington and Madgwick (1959c) showed the concentration of four major nutrients in the total foliage of Scots pine were significantly negatively related to bole girth, although because of differing proportions of new and old leaves between trees of dominant and supressed classes this would tend to occur whenever the nutrient concentration decreased with tissue age.

The within-stand variation in nutrient concentration could reflect differences in amounts of nutrients available to individual trees, even on what appears to be a relatively uniform site. Alternatively the individual trees may differ in their capacity to accumulate and utilize the nutrients in the soil. The importance of between-tree variation in

nutrient content is discussed in more detail in Chapter 8. The present results support the conclusion that, within the five study plots examined, none of the nutrients are so markedly deficient or in excess that a comparison of the five plots is unjustified.

5.3.3 Comparison of nutrient concentration between study plots

In this investigation it is assumed the five stands of radiata pine represent an age series, the younger plots closely depicting the conditions of the older plots when at the younger age. The stand mensuration parameters indicate the series represent normal stand development; the progressive dry weight distribution supports this conclusion, and the chemical analysis of the soils of each study plot indicates a comparable, non-limiting supply of all nutrients in all plots (Chapter 2).

The nutrient status of trees in the five plots can be compared most satisfactorily by examining comparable foliage samples, because the leaves mature quickly and then show little morphological change, and the age range is limited to three years. Nutrient concentrations in the foliage from each age-strata (average for nine trees per plot) are shown in Figs. 5.2 a - f. The average concentration of each nutrient in the uppermost age-strata (1965 - 1966) which contains only leaves up to 1 - year old is shown with the confidence limits for each study plot.

The mean concentrations (for 9 trees per plot) of nutrients in the uppermost age-strata differ from plot to plot, but few significant differences occur between means, partly because of large within-plot variances.

Comparison of means by Tukey's Multiple Range test (e.g. analysis for magnesium in Table 5.4) shows the

FIG. 5-2 THE CONCENTRATIONS OF MINERAL NUTRIENTS IN THE FOLIAGE OF P.RADIATA TREES FROM FIVE STUDY PLOTS

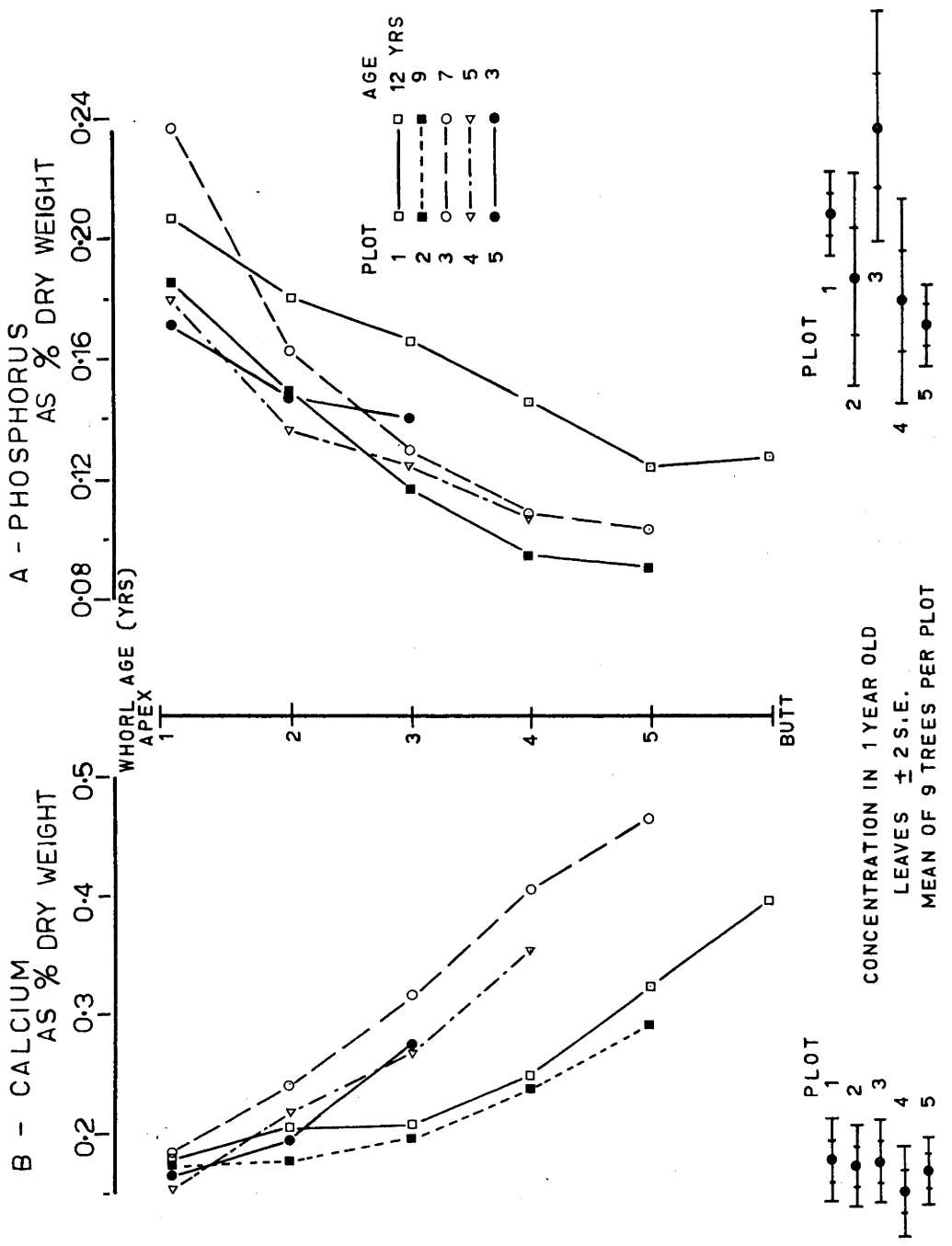


FIG. 5-2 THE CONCENTRATION OF MINERAL NUTRIENTS IN THE FOLIAGE OF P.RADIATA TREES FROM FIVE STUDY PLOTS

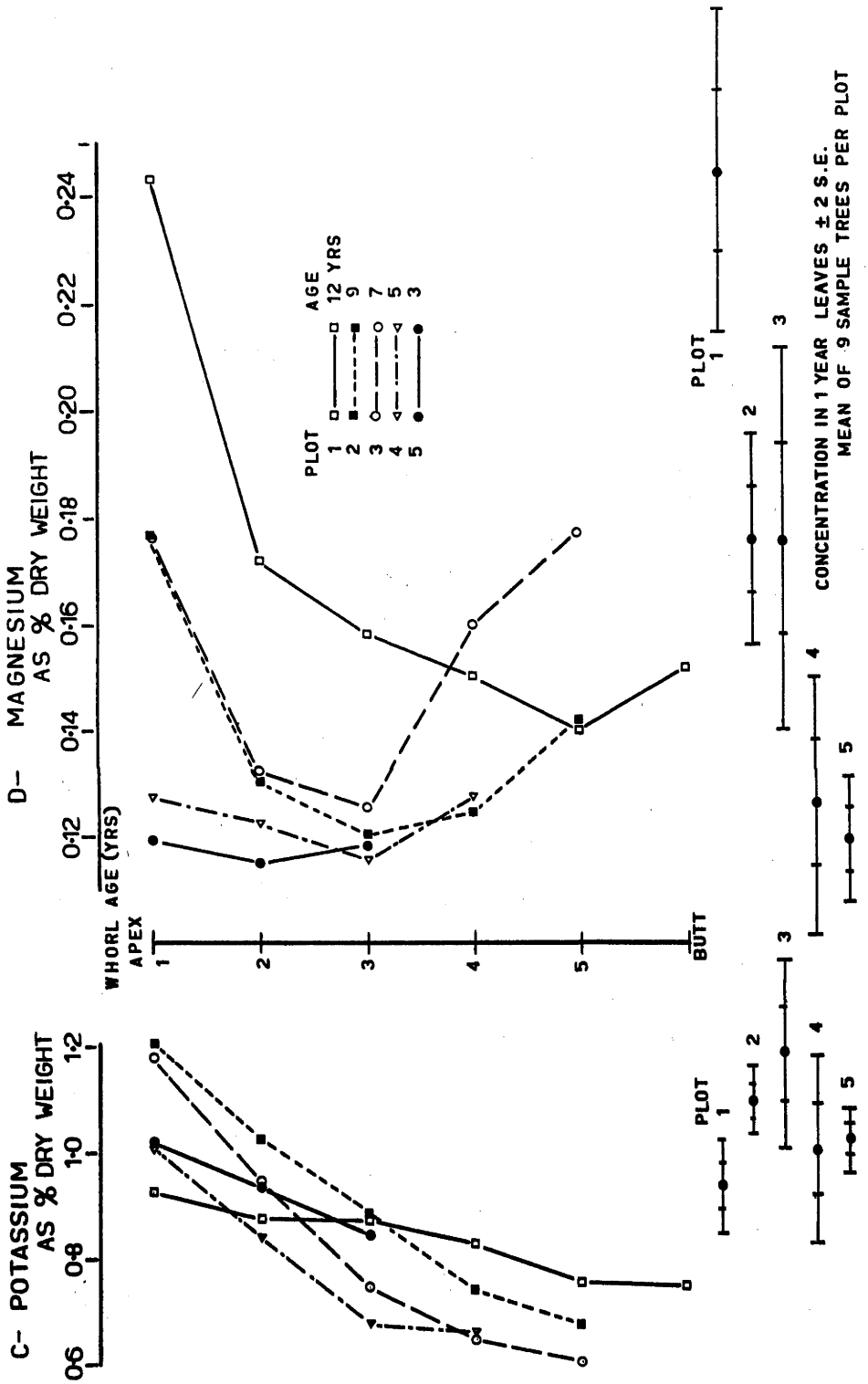


FIG. 5-2 THE CONCENTRATION OF MINERAL NUTRIENTS IN THE FOLIAGE OF P.RADIATA TREES FROM FIVE STUDY PLOTS

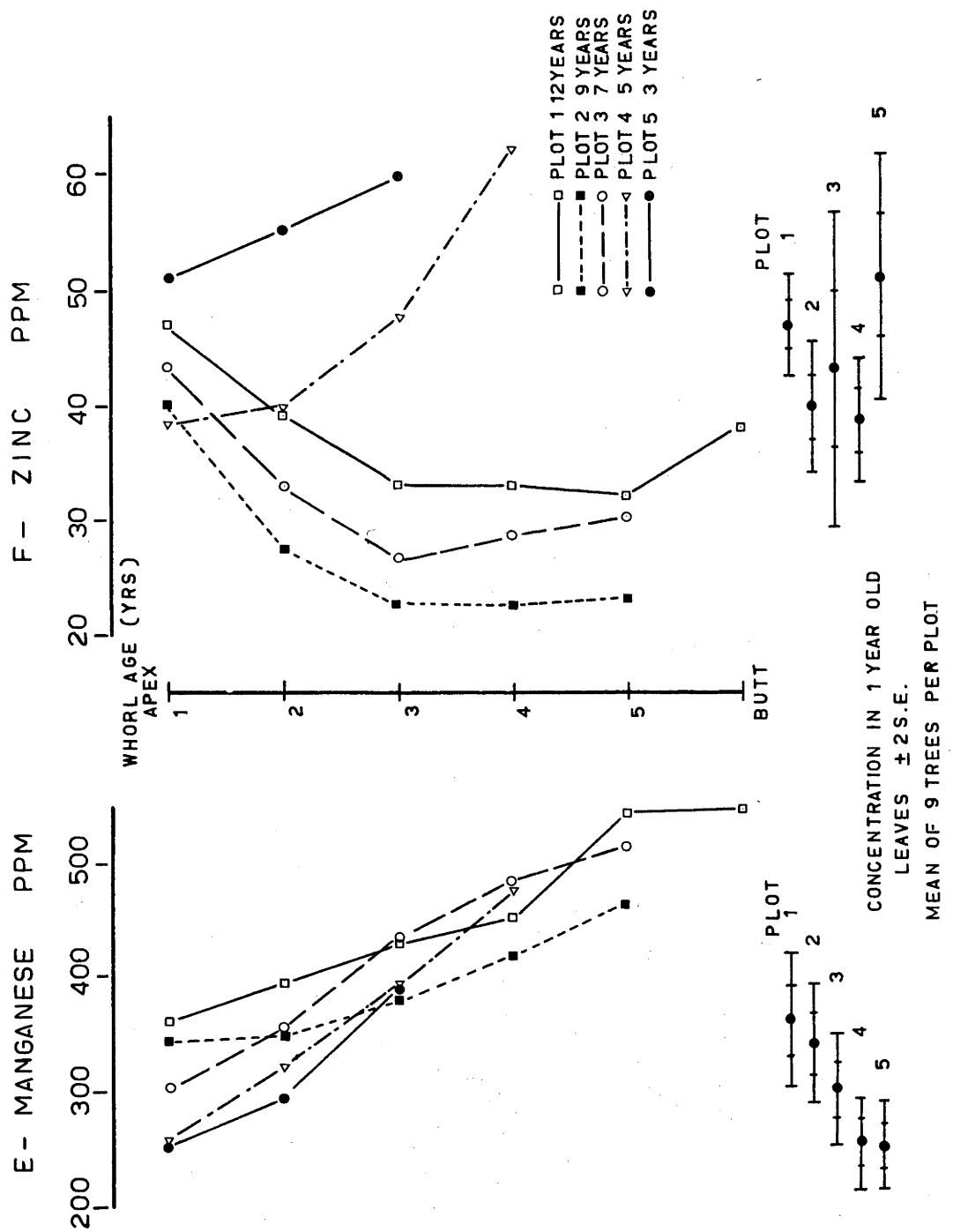


TABLE 5.4 Comparison of magnesium concentrations in 1 - year old foliage of trees in five study plots of P. radiata age series

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Mean magnesium concentration ($\bar{X}$)	0.245	0.176	0.176	0.126	0.119
S.E.$_{\bar{X}}$	0.015	0.010	0.018	0.012	0.006
S.E.$_{\bar{X}}$ x T_M 5%	0.053	0.036	0.064	0.043	0.021
S.E.$_{\bar{X}}$ x T_M 1%	0.080	0.053	0.096	0.064	0.032

Table of means differences

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Plot 1	-	-	-	-	-
Plot 2	0.069 *	-	-	-	-
Plot 3	0.069 *	0.0	-	-	-
Plot 4	0.119 **	0.050 *	0.050	-	-
Plot 5	0.126 **	0.057 **	0.057	0.007	-

* = significant at P = 0.05

** = significant at P = 0.01

T_M = Studentized range for Tukey's multiple range test.

following plot mean nutrient concentrations differ significantly:

Phosphorus:	plot 5 < plot 1,	P = 0.01
Calcium:	No significant differences	P = 0.05
Potassium:	plot 1 < plot 2,	P = 0.05
Magnesium:	plots 4 and 5 < plot 1,	P = 0.01
	plot 5 < plot 2,	P = 0.01
	plot 4 < plot 2,	P = 0.05
	plots 2 and 3 < plot 1,	P = 0.05
Manganese:	plots 4 and 5 < plot 1,	P = 0.05
Zinc:	No significant differences	P = 0.05

Phosphorus and potassium concentrations tend to increase slightly during the early years till canopy closure and then either remain more or less constant (phosphorus) or decrease (potassium). Calcium concentrations are remarkably constant through the age series; zinc also does not vary significantly. Only magnesium varies substantially and regularly through the age series, although a similar, lesser trend is evident for manganese.

The differences between plot means may be attributed to several factors, such as stand age, nutrient recycling and nutrient availability. Chemical analysis has shown only small differences in nutrient content of the soils of each plot, and these differences cannot be related directly to the variation in foliage nutrient content. Litter decomposition is substantial after age 7 years so additional nutrients released from the litter to the soil solution may have contributed to the greater concentrations of some nutrients in the foliage of older trees. There is little information available concerning the relationships between nutrient concentration and tree age, although nutrient concentration in comparable foliage samples may vary greatly from year to year (e.g. Humphreys and Kelly, 1962; Miller, 1966) without any significant trend over a long period.

The concentration of each nutrient examined changes through the tree crown, the pattern of change for each nutrient element being similar in all plots (Figs. 5.2 a - f). The average concentration of nutrients in foliage varies with the average age of leaves and also because of the influence of position within the canopy on nutrient concentration within each age class, but the effect of the latter is probably small compared with changing average leaf age (Will, 1957; Lowry and Avard, 1965).

The variation with tree age in magnesium distribution through the crown is complex, probably due to an increase with tree age in magnesium concentration in 1 - year old leaves. The concentration of magnesium does not change markedly with leaf age (Will, 1957; see also Chapter 6). The distribution of zinc through the crowns of very young trees (plots 4 and 5) differs from that in older trees (plots 1, 2 and 3), although the concentration of zinc in young leaves is similar for all tree ages. Factors contributing to a change in nutrient concentration with tissue age are discussed in Chapter 6.2.

Summary

(i) The nutrient concentrations of the sample trees have been examined so the nutrient status of the five study plots can be compared.

Average concentrations of nutrients in one - year old foliage from the apex of each tree are similar between plots, particularly for calcium and zinc. Magnesium, and to a lesser degree manganese, increases in concentration through the age-series.

(ii) Changes in average concentration of nutrients through the tree crown are also similar for each of the nutrients, except for zinc for which the pattern of change varies between very young and the older plots, and for magnesium for which again a trend with age is apparent.

(iii) No variation can readily be related directly to soil nutrients and the results of soils analysis, and it is suggested that the substantial variation between plots shown by magnesium, manganese and zinc is probably related more to progressive physiological development of the plant than to variation in soil nutrient availability.

(iv) There is no substantial evidence in the results of chemical analysis of the sample trees to indicate the five study plots are unrepresentative of normal development for the plantation.

5.3.4 Nutrient content of *P. radiata* stands

(a) General

The methods used to calculate total amounts of nutrients per tree and per unit area should take full account of the variations in nutrient concentrations in sampling components, trees and plots. As indicated previously such variation may result from (i) differences in site and environment which, although apparently slight, cannot be precisely assessed in this study, (ii) varying proportions of old and young tissues in each part of the tree, which are known to exist between trees and with tree age, and (iii) changing tree age and development, the effects of which remain unknown but for some nutrients might be important.

The evidence suggests the five study plots can be regarded as the progressive development of a single stand, and the nine sample trees in each plot adequately represent each plot. Consequently the weights of nutrients in each sample was calculated from the nutrient concentration and dry weight data. The weights of nutrients per sample were summed progressively to determine the weights of nutrients in each component and the total weight for each tree. Regression equations relating the weight of nutrients per component and per tree to bole size were then calculated.

For this purpose the weight of nutrients, i.e. the dependent variable, has been derived without substantial error, and was selected at random with respect to bole size, i.e. the independent variable.

(b) Calculation of regression equations

The several forms of regression equation which gave significant results between tree weight and bole size variables were also calculated and compared for nutrient weights for each component and the total tree.

Within each forest stand the range of component (and total) dry weight values is far greater than the range of nutrient concentrations, so nutrient weight per component is closely related to component dry weight, and is consequently also related to bole size. However, the resulting regression equations are generally less precise than the comparable dry weight equations, because nutrient concentrations are only poorly related, or are unrelated to bole size.

Consequently the same regression form as used for dry weight was adopted for the calculation of stand nutrient weight.

Log_e nutrient weight = a + b $\log_e$ (Bole B.A. x Height) -equation 3, was used for plots 1 - 4, and

Nutrient weight = a + b $\log_e$ height ----- equation 4, was used for plot 5.

The regression constant "a" and coefficient "b" used to calculate total weight of each nutrient for the five study plots are listed in Table 5.5. The significance of each total nutrient weight equation is also shown. All equations are highly significant (P = 0.01) except for weight of calcium in study plot 2 which is significant at P = 0.02.

TABLE 5.5 Regression constant and coefficient, and significance of regression equations used in the calculation of total weight of nutrients in P. radiata age series

Plots 1 - 4 Log_e nutrient weight = a + b $\log_e$ (B.A. x Height)

Plot 5 Nutrient weight = a + b $\log_e$ Height

For significance at P = 0.01 level, t (= b/S.E.$_b$) = 3.50

	Phosphorus	Calcium	Potassium	Magnesium	Manganese	Zinc
Plot 1						
a	0.175	1.287	3.222	0.890	-0.615	-3.026
b	1.184	1.173	0.854	1.125	1.010	1.144
t	19.8	17.3	8.5	18.9	20.2	13.8
Plot 2						
a	1.678	2.516	3.734	2.005	0.581	-1.961
b	0.508	0.569	0.686	0.678	0.551	0.663
t	5.0	3.4	7.7	7.9	4.3	5.4
Plot 3						
a	1.766	2.563	3.724	2.121	0.375	-1.723
b	1.033	1.174	0.997	1.058	1.085	0.933
t	12.4	9.8	8.8	7.7	6.7	6.6
Plot 4						
a	2.373	2.824	4.267	2.369	0.914	-0.834
b	0.725	0.637	0.751	0.658	0.663	0.671
t	34.5	7.1	12.9	9.6	8.5	11.5
Plot 5						
a	-1.349	-2.103	-8.792	-1.150	-0.282	-0.073
b	1.371	2.076	8.797	1.199	0.283	0.069
t	11.8	5.7	33.4	7.8	5.9	4.6

N.B. Units of measurement: Weight in grams
Basal area in square feet
Height in feet

(c) Calculation of total nutrient content per unit area

The total weight of each nutrient element in the trees of the five study plots has been calculated by solving for all trees in equations 3 (plots 1 - 4) and 4 (plots 5), using appropriate pairs of "a" and "b" values (Table 5.5). Similar equations for the weights of nutrients in each major component were also solved separately for all trees, and estimates of stand nutrient weight by components derived (Tables 5.6 a - f). These latter values were rounded slightly for their summed total to equal the total weight calculated by regression, and the relative distribution of nutrients by components was calculated for the five study plots (Tables 5.7 a - f).

In all subsequent discussions the total weights of nutrients in the P. radiata stand per unit area are values derived from repetitive solution of equations 3 and 4 for all trees in the plot, where y = total weight of nutrients per tree. For some plots the totalled weights for each component only approximately equal the total weights calculated by regression because of poor correlation for some minor components, particularly cones.

(d) Nutrient content of P. radiata component of the age-series

For each of the nutrient elements examined there is a similar broad pattern of increase in total amounts contained within the P. radiata trees with increase in stand age (Figs. 5.3 a - f), because any variation in average nutrient concentration with age is much less than the increase in stand dry weight. However there is a marked change with age in the distribution of nutrients between the major components (Table 5.7 a - f) which results in important differences in the rate of increase in weight for some nutrients, particularly after canopy closure.

FIG. 5-3 TOTAL WEIGHT OF MINERAL NUTRIENTS IN P. RADIATA TREES AT SUCCESSIVE STAGES IN THE DEVELOPMENT OF A PLANTATION

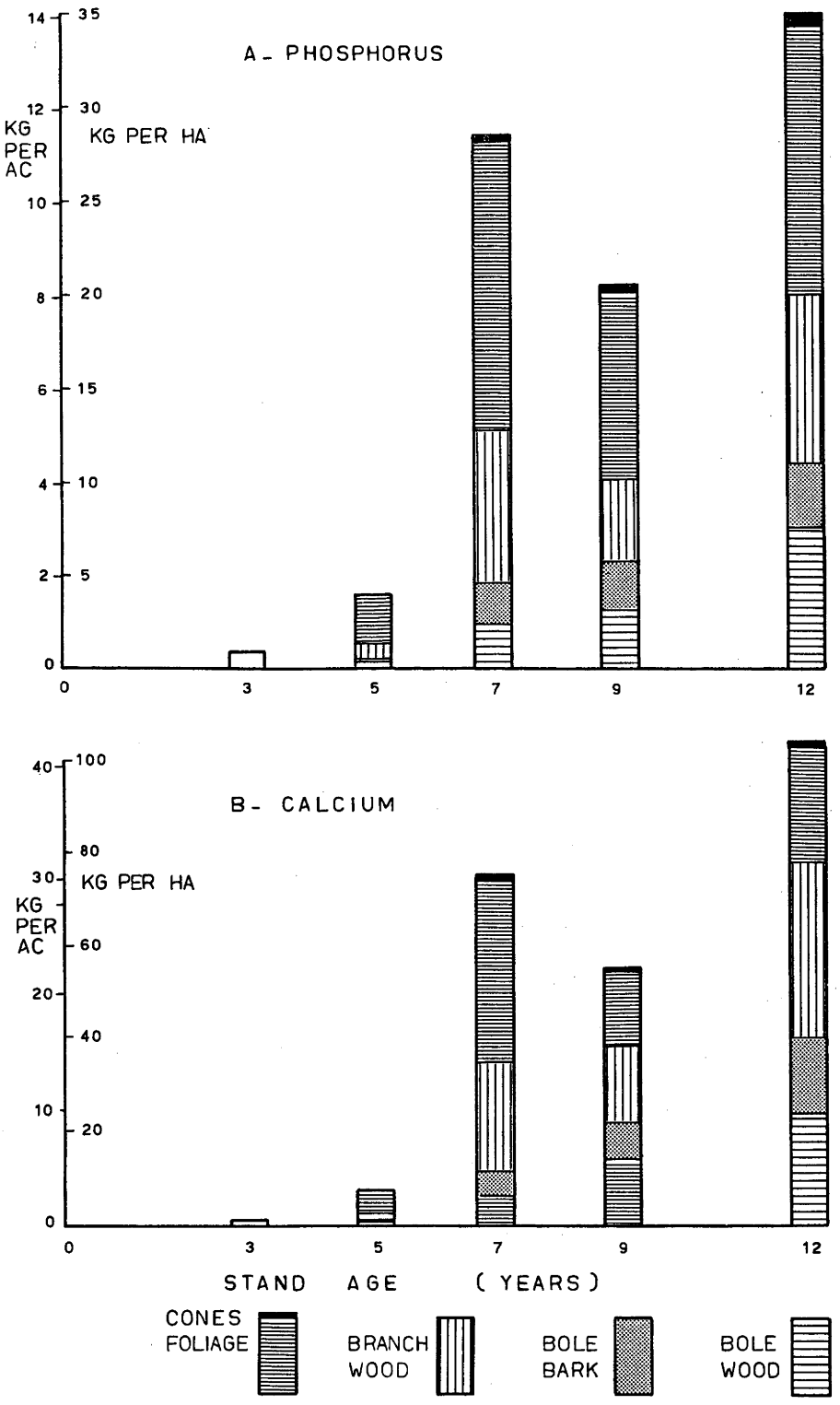


FIG. 5-3 TOTAL WEIGHT OF MINERAL NUTRIENTS IN P.RADIATA TREES AT SUCCESSIVE STAGES IN THE DEVELOPMENT OF A PLANTATION

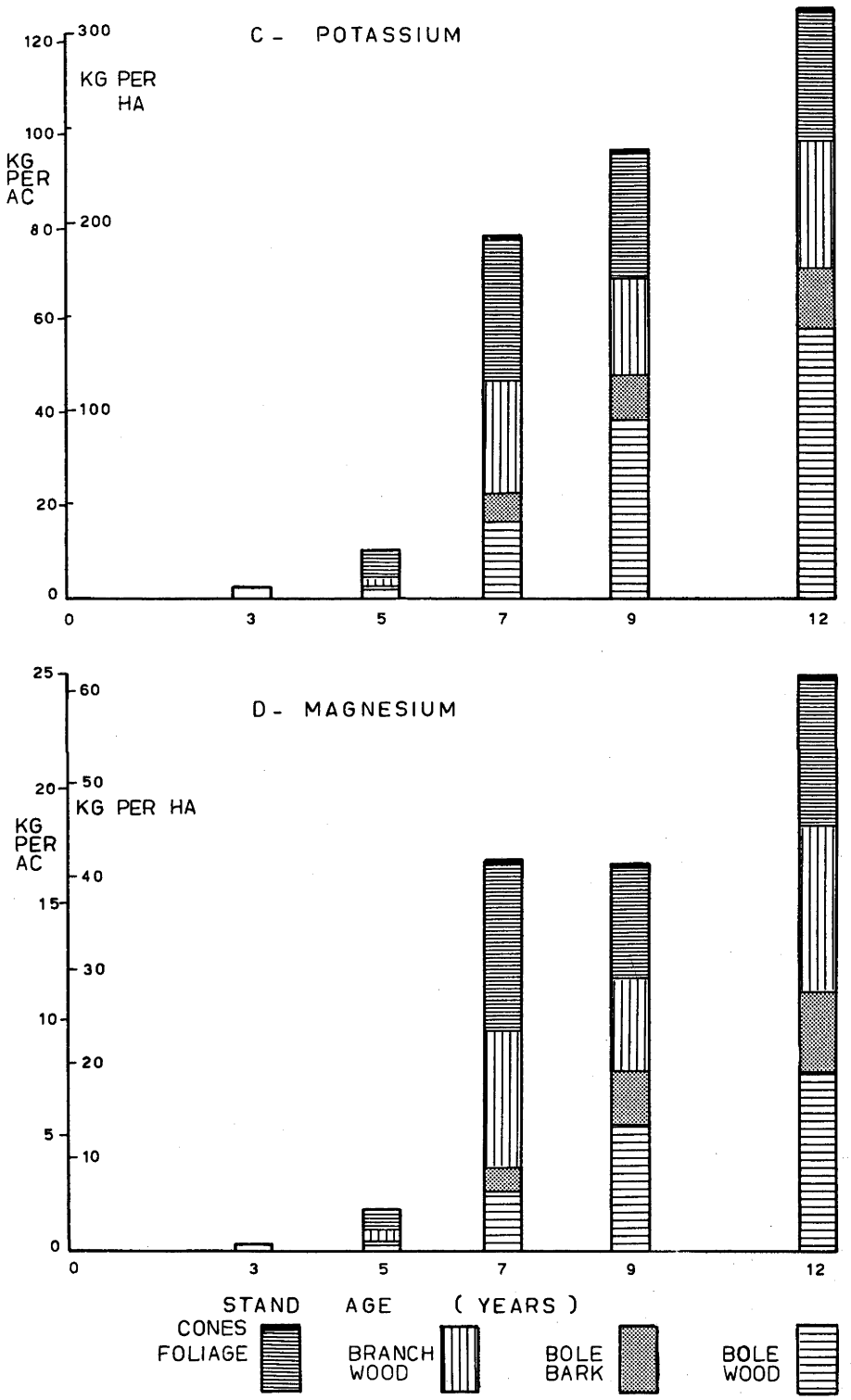


FIG. 5-3 TOTAL WEIGHT OF MINERAL NUTRIENTS IN P. RADIATA TREES AT SUCCESSIVE STAGES IN THE DEVELOPMENT OF A PLANTATION

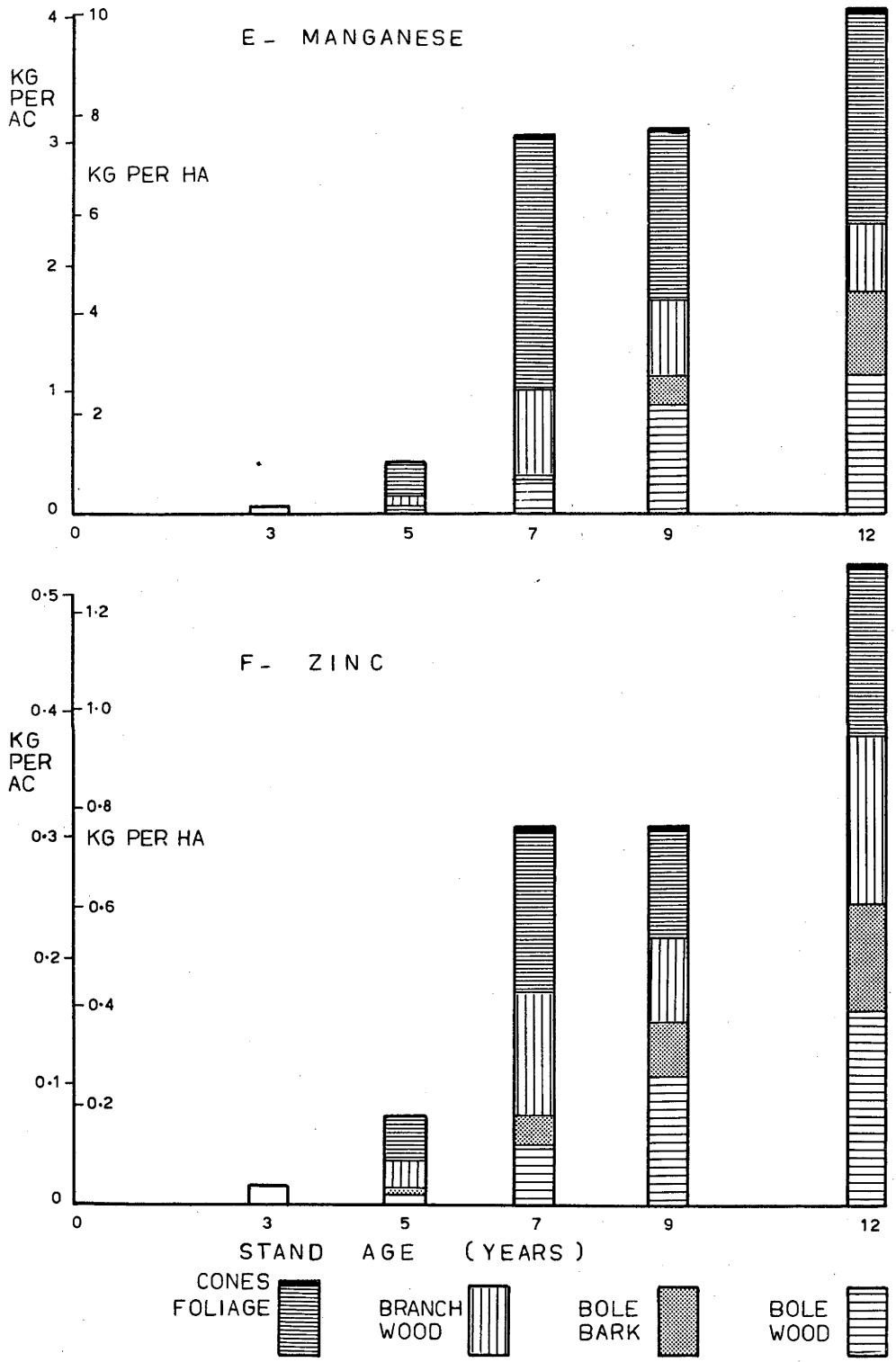


TABLE 5.6 a Total weight of phosphorus in young *P. radiata* stands (kg per ha)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	0.141	0.79	8.20	4.35	8.92
Branch leaves	0.568	2.45	14.26	9.39	13.54
Bole leaves	0.124	0.30	1.09	0.62	0.77
Bole bark	0.059	0.25	1.85	2.64	3.48
Bole wood	0.084	0.35	2.77	3.14	7.56
Cones	-	-	0.42	0.49	0.47
Total tree (by regression)	0.974	4.08	28.60	21.32	35.00

TABLE 5.7 a Distribution of phosphorus in young *P. radiata* stands (Percentage of total weight)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	14.4	19.4	28.8	20.4	25.2
Branch leaves	58.2	59.7	49.7	44.1	38.4
Bole leaves	12.7	7.2	3.8	2.9	2.2
Bole bark	6.2	6.3	6.5	12.3	9.9
Bole wood	8.6	8.4	9.7	14.8	21.4
Cones	-	-	1.5	2.4	1.4
Total tree	100.0	100.0	100.0	100.0	100.0

TABLE 5.6 b Total weight of calcium in young P. radiata stands (kg per ha)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	0.17	1.48	23.3	14.3	36.9
Branch leaves	0.79	4.35	38.9	17.8	25.3
Bole leaves	0.22	0.49	1.0	0.6	0.7
Bole bark	0.11	0.54	4.9	7.6	17.3
Bole wood	0.10	0.59	6.5	14.3	23.8
Cones	-	-	0.1	0.1	0.2
Total tree (by regression)	1.38	7.41	76.6	55.8	104.2

TABLE 5.7 b Distribution of calcium in young P. radiata stands (Percentage of total weight)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	12.6	20.1	30.4	25.7	35.4
Branch leaves	56.8	58.9	50.8	31.9	24.3
Bole leaves	15.6	6.6	1.3	1.2	0.7
Bole bark	7.9	7.3	6.4	13.7	16.6
Bole wood	7.1	8.0	8.4	25.7	22.8
Cones	-	-	0.1	0.2	0.2
Total tree	100	100	100	100	100

TABLE 5.6 c Total weight of potassium in young *P. radiata* stands (kg per ha)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	1.10	6.20	60.8	45.1	65.7
Branch leaves	3.09	12.40	69.7	62.1	65.7
Bole leaves	0.64	1.56	4.9	3.6	2.8
Bole bark	0.38	1.58	15.4	28.8	31.4
Bole wood	0.84	4.42	40.6	95.1	143.3
Cones	-	-	1.3	2.0	1.4
Total tree (by regression)	6.05	26.04	193.5	238.9	314.8

TABLE 5.7 c Distribution of potassium in young *P. radiata* stands (Percentage of total weight)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	18.2	23.7	31.4	18.9	20.9
Branch leaves	51.0	47.6	36.0	26.0	20.9
Bole leaves	10.5	6.0	2.6	1.5	0.9
Bole bark	6.2	6.1	8.0	12.1	10.0
Bole wood	14.0	17.0	21.0	39.8	45.5
Cones	-	-	0.7	0.8	0.4
Total tree	100	100	100	100	100

TABLE 5.6 d Total weight of magnesium in young *P. radiata* stands (kg per ha)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	0.18	1.31	14.43	9.69	17.79
Branch leaves	0.44	2.03	17.64	11.00	15.15
Bole leaves	0.10	0.30	0.64	0.69	0.64
Bole bark	0.07	0.37	2.84	5.66	8.43
Bole wood	0.12	0.64	6.20	13.57	19.00
Cones	-	-	0.32	0.32	0.57
Total tree (by regression)	0.89	4.55	42.25	41.76	61.80

TABLE 5.7 d Distribution of magnesium in young *P. radiata* stands (Percentage of total weight)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	19.8	28.9	34.2	23.2	28.8
Branch leaves	48.6	44.8	41.8	26.3	24.5
Bole leaves	11.0	6.6	1.5	1.7	1.0
Bole bark	7.8	8.1	6.7	13.5	13.6
Bole wood	12.9	14.1	14.7	32.5	30.7
Cones	-	-	0.8	0.8	0.9
Total tree	100	100	100	100	100

TABLE 5.6 e Total weight of manganese in young *P. radiata* stands (kg per ha)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	0.022	0.19	1.63	1.46	2.36
Branch leaves	0.119	0.67	4.92	3.31	4.25
Bole leaves	0.027	0.07	0.14	0.12	0.13
Bole bark	0.010	0.04	0.19	0.55	0.67
Bole wood	0.017	0.09	0.69	2.20	2.79
Cones	-	-	0.01	0.01	0.01
Total tree (by regression)	0.195	1.04	7.66	7.76	10.16

TABLE 5.7 e Distribution of manganese in young *P. radiata* stands (Percentage of total weight)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	11.2	17.9	21.3	18.9	23.2
Branch leaves	60.9	64.4	64.5	42.7	41.8
Bole leaves	14.6	6.4	1.8	1.6	1.2
Bole bark	4.5	3.2	2.5	7.1	6.6
Bole wood	8.9	8.9	9.0	28.2	27.4
Cones	-	-	0.1	0.1	0.1
Total tree	100	100	100	100	100

TABLE 5.6 f Total weight of zinc in young *P. radiata* stands (kg per ha)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	0.007	0.054	0.250	0.17	0.34
Branch leaves	0.022	0.082	0.320	0.21	0.33
Bole leaves	0.005	0.007	0.017	0.02	0.02
Bole bark	0.002	0.012	0.057	0.11	0.22
Bole wood	0.005	0.025	0.124	0.26	0.39
Cones	-	-	0.002	0.00	0.01
Total tree (by regression)	0.042	0.180	0.766	0.77	1.29

TABLE 5.7 f Distribution of zinc in young *P. radiata* stands (Percentage of total weight)

Component	Plantation stand age (years)				
	3	5	7	9	12
Branch wood	19.1	30.2	32.7	22.5	26.3
Branch leaves	51.3	44.7	41.2	26.8	25.2
Bole leaves	11.1	4.7	2.3	1.8	1 3
Bole bark	8.2	6.7	7.3	13.9	16.6
Bole wood	10.3	14.0	15.8	33.2	30.2
Cones	-	-	0.3	0.5	0.1
Total tree	100	100	100	100	100

At 5 years the P. radiata trees weigh (dry) only 5% of the total weight at 12 years, but the nutrients contained at age 5 years vary from 7% for calcium to 14% for zinc of the weight at 12 years, depending on the relative concentration of each in the bole and canopy components. The six fold increase in stand weight between 5 and 7 years, shared nearly equally between bole and canopy components (Chapter 2) results in similar increases in the weights of each nutrient. At age 7 years the P. radiata trees weight 50 m tons per ha and contain 29, 77, 194, 42, 7.5 and 0.8 kg per ha of P, Ca, K, Mg, Mn, and Zn respectively, the rate of increase in nutrient content during the 5th to 7th years being 12, 30, 84, 19, 3.3 and 0.3 kg per ha per annum respectively.

For two years after 7 years of age the rate of increase in weight of bole components becomes slightly greater and then continues at a level similar to that between 5 - 7 years. In contrast, the increase in weight of foliage changes markedly as competition between trees increases. After 8 years, the weight of leaves and live branches becomes constant and the weight of dead branches increases only slowly. Since the concentration of all nutrients is greatest in the foliage, the rate of increase is greater for all nutrients between ages 5 and 7 years than at any other time.

The pattern of nutrient distribution varies after canopy closure, depending on the relative concentrations between foliage, branch and bole components, and the changes in nutrient concentration within each component with increasing tree age. For example, the weight of phosphorus, calcium and potassium in the foliage as a proportion of the respective totals in the trees, varied little at 3 years, being from 51 to 58% of the total for each nutrient; but at canopy closure the proportion of phosphorus and calcium in the branch leaves were similar (50 and 51%) whilst only 36% of the potassium was in branch leaves. Finally, by 12 years 36, 24 and 21% of total P, Ca and K respectively was in

branch leaves. The pattern is further confused by pruning of the lower branches in plots 1 and 2. As a result of these factors there is substantially less phosphorus and calcium in the P. radiata stand at age 9 years than at 7 years. Magnesium, manganese and zinc remain fairly constant between the two periods, and there is an increase in the amount of potassium by 9 years due mainly to the relatively greater proportion of this element in young leaves.

Although less nutrients are contained in the trees of plot 2 (9 years) than in an unpruned stand of the same age, the nutrients in plot 1 are less as a result of pruning only by the weight of nutrients that would be present in the dead branches below 3 metres height.

The rate of increase in stand nutrient content beyond age 12 years depends primarily on the rate of bole increase which is relatively constant for at least a further 10 - 12 years, and the average nutrient concentration of the bole which, for many nutrients, may decrease substantially. A more detailed examination of the rate of nutrient accumulation is made for the total biomass in Chapter 5.5.

5.3.5 Summary

(i) Study plots have been located in five P. radiata plantation stands selected as an age series from 3 to 12 years. Nine trees were sampled from each plot, subdivided by components and age-strata, and estimates derived for the concentrations of phosphorus, potassium, calcium, magnesium, manganese and zinc in each unit.

The weight of nutrients in each sample tree, and hence for each stand, were calculated. From these data, estimates of nutrient accumulation rates and the effects of stand development on nutrient accumulation and distribution were derived.

(ii) The patterns of nutrient distribution within the sample trees were similar to those observed in other P. radiata stands and for other species. The concentrations of nutrients usually declined in the following order-stem leaves, branch leaves, bole bark, branch wood, female cones and bole wood.

The concentrations of phosphorus, potassium, magnesium and zinc decrease in all components with increasing distance from the tree apex (i.e. increasing average component age); calcium and manganese increase with distance from the apex in the crown components and were virtually constant in the bole components.

(iii) The concentrations of each nutrient, either in comparably aged tissues or the average for each component, varied substantially between trees. Potassium and phosphorus tended to increase, whilst calcium and magnesium concentrations decreased slightly with tree size, as reported in some other studies.

(iv) When the concentrations of nutrients in young foliage samples for trees in the five plots were compared, only magnesium varied significantly and consistently through the age series. The concentrations of magnesium increased steadily through the age series, from 0.12 to 0.24% in the 1 - year old foliage, although the reason for the increase is unclear.

Phosphorus and manganese concentrations also tended to increase with tree age, but the increase was irregular and not supported by other results either in this study or in the literature.

(v) Total dry weight production reaches a maximum immediately prior to canopy closure when foliage production is also at a maximum. Since the concentration of each nutrient studied is appreciably greater in the foliage than in other components, the accumulation of nutrients within

the P. radiata stand is also at a maximum immediately before canopy closure (age 6 - 7 years in the present study).

(vi) For those nutrients substantially more concentrated in the lower crown than in the bole, e.g. phosphorus and calcium, the trees contained less at 9 years than at age 7 years due to pruning the lowest branches to a height of 3 metres.

(vii) The accumulation of nutrients within the tree stand after 12 years is determined largely by their concentrations within the bole. The average concentrations in the bole wood of some nutrients, particularly potassium and phosphorus, probably decreases as the proportion of heartwood of low concentration increases and so the accumulation rate of those nutrients is relatively less than the rate of bole increase.

5.4 RESULTS AND DISCUSSION. NUTRIENT CONTENT OF THE GROUND VEGETATION AND LITTER LAYERS

5.4.1 Concentration of nutrient elements in ground vegetation and litter layers

The average concentrations of several nutrients determined for the ground vegetation and litter layers in each of the five study plots is presented in Table 5.8. The number of quadrats, out of twenty quadrats per plot, from which material of each category was collected is listed to indicate the relative reliance given to the concentration values.

The progressive development of the litter layers and decline of ground vegetation previously discussed (Chapter 2) is reflected in the change in nutrient concentration values with increasing stand age, although only a few of the categories identified are present in enough quadrats to allow statistical comparisons between plots. For example, the values of phosphorus and potassium in the native grasses are greatest in the youngest plot but manganese increases with plot age.

TABLE 5.8 Average concentration of nutrient elements in subordinate vegetation and litter layers beneath *P. radiata* age series

Category	Stand age	No. of samples	Nutrient concentration P %	Ca %	K %	Mg %	Mn ppm	Zn ppm
Subordinate vegetation								
Bracken fern	3	1	0.07	0.25	0.52	0.26	205	9
	5	2	0.04	0.32	0.09	0.26	270	10
	7	4	0.02	0.17	0.10	0.15	110	6
	9	11	0.03	0.25	0.07	0.17	230	16
	12	4	0.03	0.30	0.08	0.18	270	14
Grasses	3	18	0.15	0.17	0.91	0.13	160	24
	5	18	0.14	0.17	0.84	0.13	190	25
	7	16	0.13	0.18	0.80	0.14	260	26
Other	3	2	0.07	0.56	0.47	0.25	280	28
	5	4	0.07	0.35	0.44	0.18	180	26
Litter layers								
Leaf litter	3	5	0.08	0.56	0.24	0.17	220	28
	5	16	0.09	0.40	0.26	0.16	275	27
	7	20	0.09	0.37	0.23	0.16	250	24
	9	20	0.09	0.44	0.22	0.17	440	24
	12	20	0.11	0.50	0.29	0.14	550	32
Decomposing litter	9	20	0.08	0.49	0.18	0.19	440	32
	12	20	0.11	0.58	0.24	0.19	640	43
Branch wood	9	12	0.02	0.19	0.09	0.09	100	18
	12	12	0.01	0.17	0.07	0.07	90	18

FIG. 5-4 CHANGES WITH AGE IN THE AMOUNTS OF MINERAL NUTRIENTS IN THE GROUND LAYERS OF A P. RADIATA PLANTATION

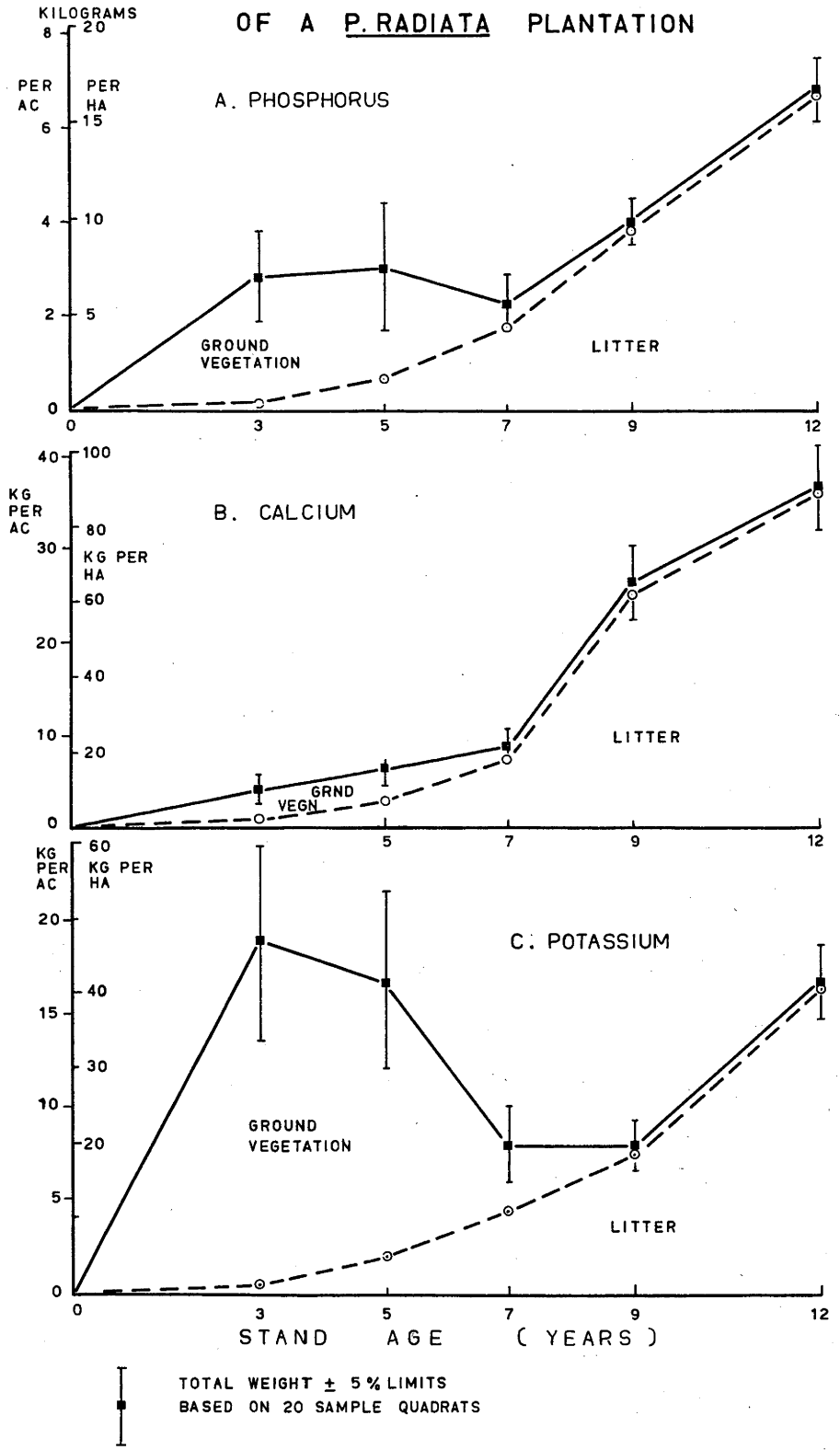
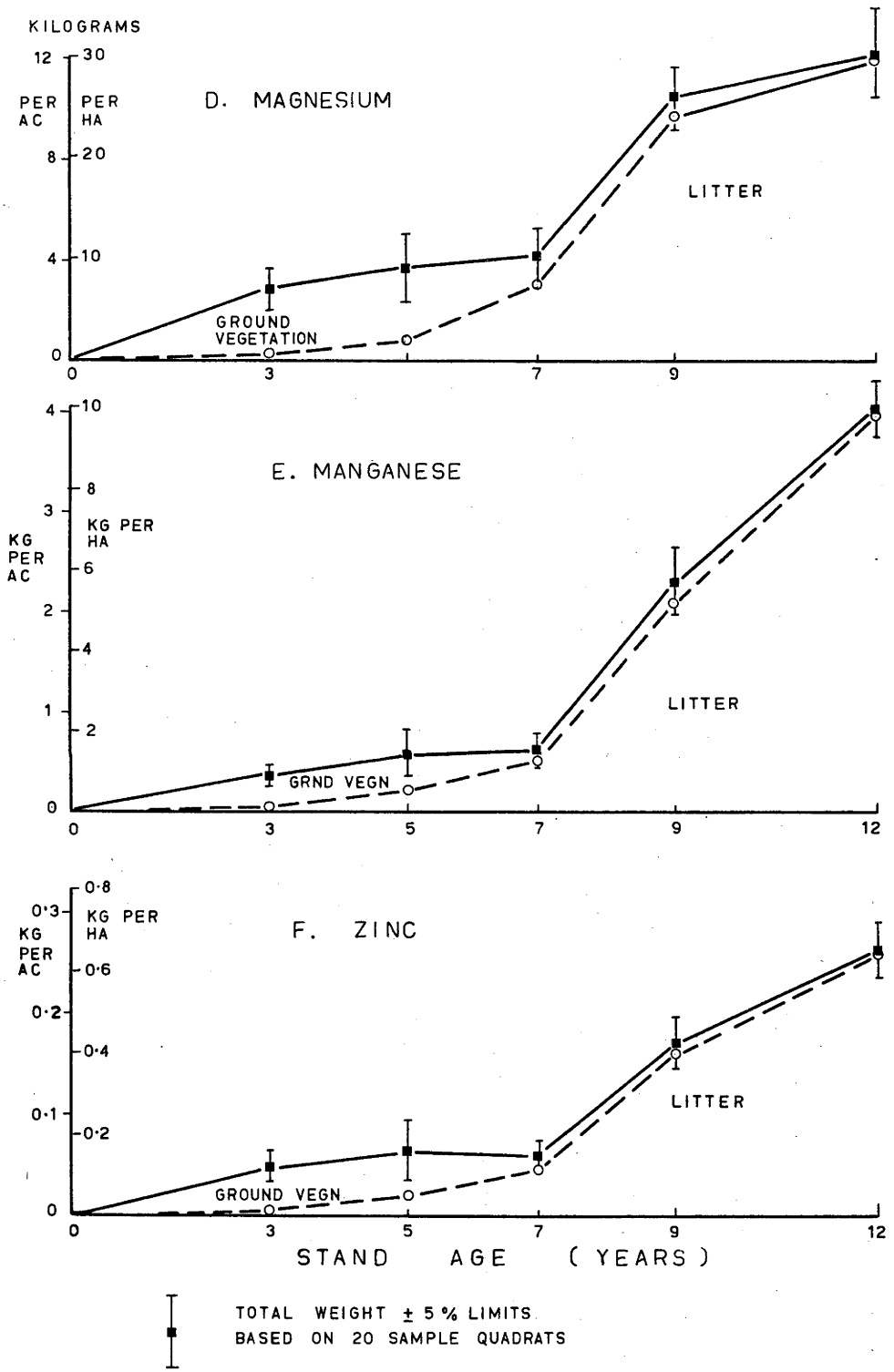


FIG. 5-4 CHANGES WITH AGE IN THE AMOUNTS OF MINERAL NUTRIENTS IN THE GROUND LAYERS OF A P. RADIATA PLANTATION



The concentration of most nutrients determined in the grass samples is large, comparing closely with the levels found in young pine leaves. Phosphorus (0.15%) and potassium (0.9%) particularly are greater than might be expected from the dead and coarse appearance of the grass tussocks. In contrast, the bracken fonds had very low values for most nutrients, partly due to the extremely low values for their stalks.

Nutrient concentrations in the upper litter layers on the forest floor depend mainly on the abundance of recently fallen material, the rate of tissue decomposition and nutrient solubility. For most nutrients examined, the concentration in fresh litter of the older plots (mainly pine leaves) is close to the value reported for the oldest living pine leaves. In the younger plots the litter material contained a higher proportion of woody material, bracken fern, etc and this has influenced the average concentration of nutrients.

The decomposing (F) layer present in the two oldest plots contains fragmented pine leaves, bark, male cones etc with only a small proportion of non-pine material. The nutrient concentrations in this layer are closely related to that of the undecomposed L - layer, the differences between the two layers giving some indication of relative rate of nutrient release (see Chapter 5.4.3).

5.4.2 Accumulation of nutrients in ground vegetation and litter layers

The total weight of each nutrient present in the ground vegetation and litter layers of the five study plots is shown in Figs. 5.4 a - f.

For each nutrient examined the amount contained in the litter layers on the forest floor increases through the age-series as the total amount of litter increases. Most nutrients accumulate rapidly between 7 and 9 years after which the rate of accumulation decreases.

The amount and distribution of nutrients present in the ground vegetation varies markedly between nutrients and between ages, due to the varying proportions of each category of vegetation and the concentrations of nutrients in each. For example, the amount of potassium in the subordinate vegetation at 3 - 5 years is very large (45 kg per ha) because of the weight of grass present and the relatively large concentration of potassium; alternatively, the concentration of calcium in grass is less than in other material and so the total weight of calcium present at 3 years is small.

The rates of accumulation of mineral nutrients in the total organic matter of ground vegetation and litter layers during the first three years after pine plantation establishment may be very large, although the amount accumulated, mainly in the understorey vegetation, is usually small compared with the amount in the litter layers in later years. For no mineral nutrient examined is there a marked increase in the amount contained in the organic material subordinate to the pine stand during ages 5 - 7 years when the growth of pine trees is at a maximum; the amount of several nutrients, particularly potassium, tended to decrease during this period.

5.4.3 Accumulation of nutrients in ground layers after 12 years

From the ninth to the twelfth year of age the understorey vegetation contributed little to the amounts of nutrients in the total organic matter of the ground layers. Observations in other older stands show the understorey vegetation remains relatively insignificant until after 25 - 30 years when, particularly after heavy thinning, the tree crowns are more sparce and an understorey layer of pine regeneration and other vegetation may develop.

Since the amount of litter falling each year does not vary greatly after 10 years and the amount of litter present is fairly constant after 12 years, litter decomposition is then in approximate balance with input. From the weight of litter present at a plantation age of 12 years, an average turnover period from fresh litter to incorporation within the mineral soil is estimated as about three years (Chapter 2).

Data of nutrient content for old and decaying foliage are drawn from all sources in the present study (Table 5.9) so the rate of nutrient release relative to organic matter breakdown can be examined. Potassium is the only nutrient with a smaller concentration in the decomposing layers than in fresh litter, and phosphorus concentrations remain nearly constant throughout. For all other nutrients, the concentrations progressively increase with litter age and the degree of decomposition, indicating lesser solubility and possibly a closer association of these elements with the more lignified and resistant leaf constituents. However, the accumulation of those nutrients must be considered relative to total organic matter decomposition. When estimates of total input are compared with amounts in all litter layers at age 12 years there is a turnover period of not more than 5 years for all nutrients.

These results contrast with those of Attiwill (1968), particularly with reference to phosphorus. Attiwill compared the relative rates of nutrient release from eucalypt litter with results reported for Russian hardwoods and concluded the cycles for phosphorus within the two plant systems were basically dissimilar. He considered the rate of phosphorus release was rapid for Russian hardwoods because of the large phosphorus concentration in fallen leaves, whilst in eucalypts most phosphorus in the leaves is recirculated prior to leaf fall and consequently the phosphorus remaining in eucalypt litter is relatively

resistant to release. However most phosphorus in P. radiata foliage is also lost before leaf fall, but the rate of release of the amount remaining appears to be at least as great as for calcium and magnesium.

Attwill infers the mobility (i.e. rate of removal from litter) of each nutrient is markedly different one from the other, for example quote " ... the order of mobility is..... Na > K > Ca > Mg > P". This conclusion is based on calculations of the loss of each nutrient relative to the decrease in litter dry weight (Attiwill's Table 5). In the first part of Table 5 the differences in release rates for phosphorus, magnesium and calcium are apparently great, but each rate has been calculated from other data (his Tables 1 and 2) which show no statistically significant change in the concentration of any of those nutrients in decomposing litter, or in branch wood and leaves separately, over a period of two years. The second part of his Table 5 shows less marked differences in relative release of the three nutrients, but the values reported are calculated from two other parameters (annual litter fall and content of litter layers) which are each independently subject to statistical error and only small changes in either would substantially alter the apparent pattern of release.

Consequently, while certain trends may be apparent, it is unlikely the rates of release of calcium, magnesium and phosphorus are statistically different. Thus, the results reported for Russian hardwoods (Remezov, 1961; Marchenko and Karlov, 1962), for E. obliqua (Attiwill, 1968) and for P. radiata (Table 5.9) all indicate that in the process from leaf maturity through abscission to complete decomposition, some nutrients are quickly removed, either by recirculation within the tree or by leaching, but where the nutrient elements are closely associated with tissue structure their release is more closely related to the decomposition of organic material. Potassium occurs in plants principally as

TABLE 5.9 Changes in nutrient content of dead leaves and litter under closed canopy P. radiata stands as an indicator of rate of release

Nutrient	Average concentration in progressively older leaves of 12 year old study plot			
	Old leaves on tree (Chapt. 5.3, 6.2)	Fresh litter (Chapt. 6.3.2)	L-layer (present data)	F-Layer (present data)
Phosphorus (% dry weight)	0.08	0.10	0.107	0.104
Calcium (% dry weight)	0.50	0.40	0.49	0.58
Potassium (% dry weight)	0.40	0.40	0.30	0.23
Magnesium (% dry weight)	0.16	0.14	0.14	0.20
Manganese (ppm)	500	350	550	650
Zinc (ppm)	30	25	32	43

soluble inorganic salts (Nason and McElroy, 1963) and is readily redistributed or leached. Phosphorus occurs in both organic and inorganic forms, while calcium and magnesium both occur primarily in organic forms, usually as large and relatively immobile organic compounds. Species probably differ in the proportion of the more soluble nutrients redistributed or leached out prior to leaf fall, but these may also be influenced by the relative availability of those nutrients. Variation in environment probably has a greater influence on rate of litter breakdown and consequent nutrient release than differences between species in the composition of leaves.

5.4.4 Summary

(i) The amounts of nutrients accumulated within the understorey vegetation vary depending on the amounts of each species present and their nutrient concentration; maximum accumulation was reached within 3 - 5 years after plantation establishment and thereafter decreased.

(ii) Competition for nutrients by the pine trees and other vegetation may be significant on nutrient deficient sites; the ground vegetation contained more of the nutrients investigated until age 5 years. The declining understorey vegetation provides a source of nutrients for growth of pines in later years.

(iii) The amount of nutrients contained in the litter layers increased through the age series to 12 years as the dry weight of litter increased, but was probably nearly constant thereafter.

(iv) The relative concentrations of each nutrient in the old leaves, fresh litter and decomposing litter indicates the more soluble nutrients, potassium and phosphorus, are returned quickly to the soil from the litter layers. The other nutrients tended to accumulate in the

decomposing litter, but this probably only delayed their return to the soil by 2 - 3 years.

5.5 CONCLUSIONS: NUTRIENT ACCUMULATION THROUGH THE AGE SERIES

As a P. radiata plantation grows from small seedlings on almost bare ground to a high forest fully dominating the site, the amounts of each mineral element accumulated within the total organic matter also increase. The growth patterns for the four distinct but mutually related layers in the plantation stand, viz. canopy, bole, litter and understorey, have been described (Chapter 2). The accumulation of nutrients in each layer has been calculated from their concentrations in each component and these data can be combined to illustrate the total accumulation of nutrients above ground level as the plantation matures (Figs. 5.5 a - f). Initially nutrients are concentrated in the ground vegetation because this layer amounts to nearly 80% of the total biomass at 3 years (Table 5.10), but as the stand matures the distribution of nutrients changes depending on the distribution of organic matter and the average concentration of nutrients in each layer. For example, at 12 years the canopy is 21.5% of the total biomass and contains 33 - 46% of the total for all nutrients determined, the bole is 66% of the biomass and contains only 21% of the total phosphorus and calcium but 50% of all potassium; at that time the litter layer which is only 12.5% of the biomass contains 11.6% of the potassium and 46% of the calcium above ground.

The total amounts of each nutrient contained above ground in the 12 year old plantation biomass (52, 195, 350, 92, 20 and 2 kg per ha of P, Ca, K, Mg, Mn and Zn respectively) are not great, many studies have reported greater total amounts (e.g. Ovington and Madgwick, 1959c; Will, 1964) even allowing for the absence of estimates for

FIG. 5-5 THE NUTRIENT CONTENT OF ORGANIC MATTER IN P.RADIATA PLANTATIONS

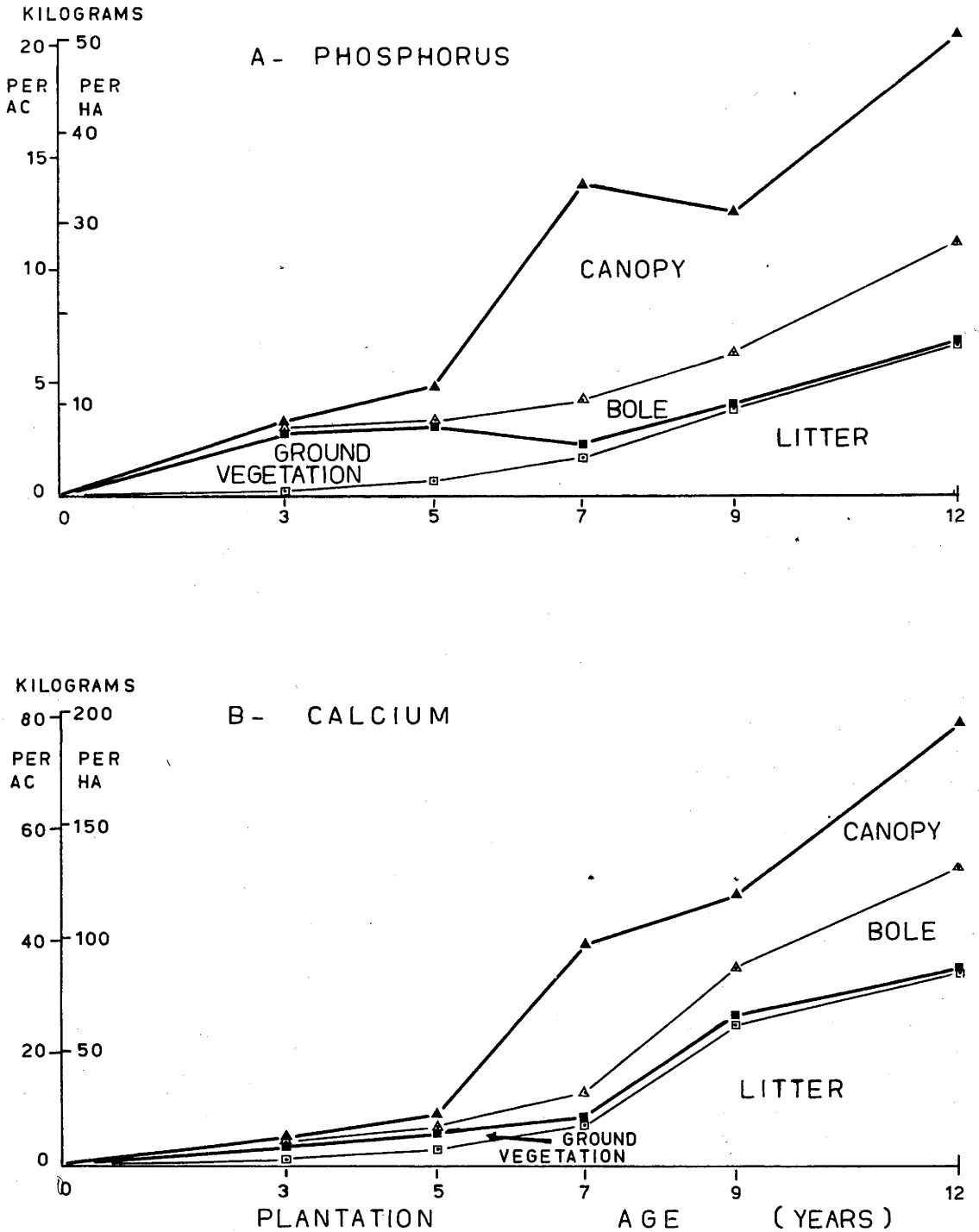


FIG. 5-5 THE NUTRIENT CONTENT OF ORGANIC MATTER IN P.RADIATA PLANTATIONS

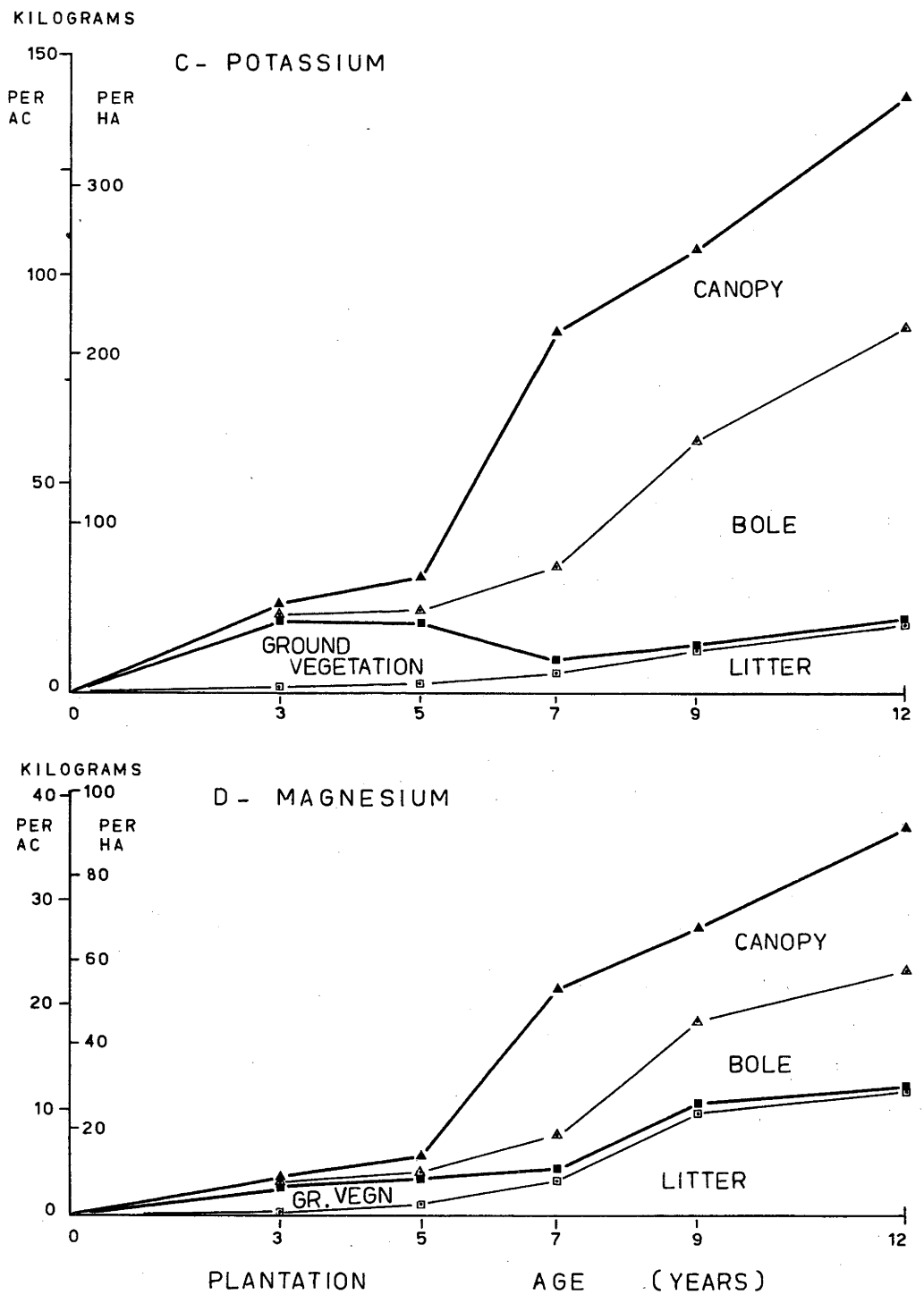


FIG. 5-5 THE NUTRIENT CONTENT OF ORGANIC MATTER IN P. RADIATA PLANTATIONS

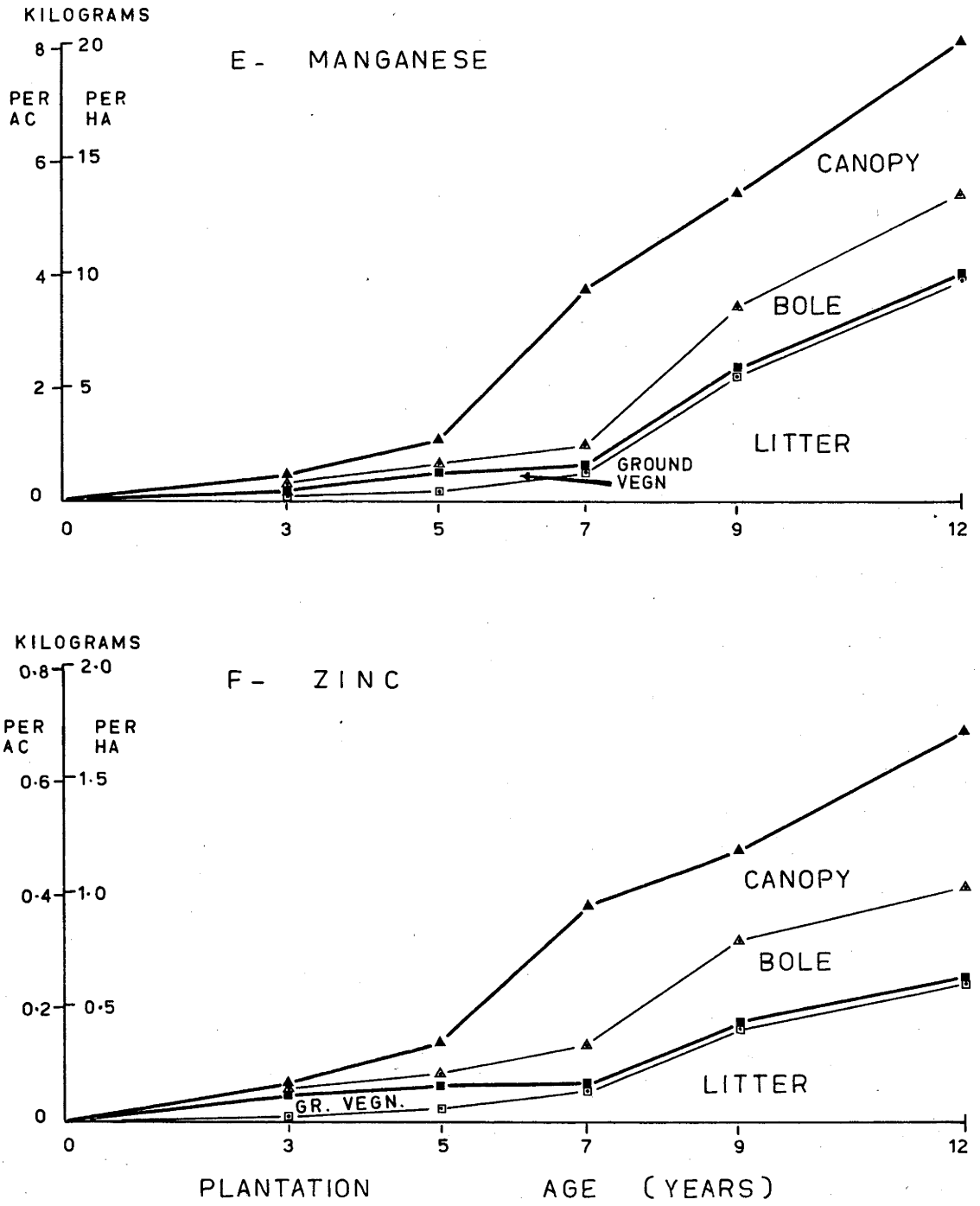


TABLE 5.10 Distribution of mineral nutrients through the main above ground layers of P. radiata plantation stands (as percentage of above-ground total)

	Plantation stand age (years)				
	3	5	7	9	12
Dry weight					
Canopy	9.4	26.6	47.0	21.8	21.5
Bole	5.2	19.2	41.6	60.6	65.7
Ground vegn.	78.7	39.3	3.2	1.4	0.3
Litter	6.7	14.9	8.2	16.2	12.5
Phosphorus					
Canopy	10.5	29.8	70.1	49.6	46.1
Bole	1.8	5.2	13.5	18.7	21.4
Ground vegn.	83.9	51.1	4.1	1.0	0.5
Litter	3.8	13.9	12.3	30.7	32.0
Calcium					
Canopy	9.7	28.0	66.8	27.6	32.5
Bole	1.7	5.1	11.6	18.3	21.0
Ground vegn.	66.6	34.7	3.1	2.3	0.6
Litter	22.0	32.2	18.5	51.8	45.9
Potassium					
Canopy	9.2	29.8	64.5	43.3	38.7
Bole	2.3	8.9	26.3	47.0	49.6
Ground vegn.	86.5	53.7	4.0	0.3	0.1
Litter	2.0	7.6	5.2	9.4	11.6
Magnesium					
Canopy	9.0	25.9	63.3	33.1	37.4
Bole	2.4	7.4	17.2	28.6	29.9
Ground vegn.	79.7	44.8	4.5	2.9	0.8
Litter	8.9	21.9	15.0	35.4	31.9
Manganese					
Canopy	15.8	37.0	73.8	37.0	33.7
Bole	2.3	5.1	9.5	20.5	17.2
Ground vegn.	73.5	36.9	3.2	2.0	0.5
Litter	8.4	21.0	13.5	40.5	48.6
Zinc					
Canopy	21.2	41.7	64.6	34.0	40.7
Bole	4.5	10.8	19.5	30.7	21.1
Ground vegn.	66.7	33.1	3.2	1.5	0.3
Litter	7.6	14.4	12.7	33.8	37.9

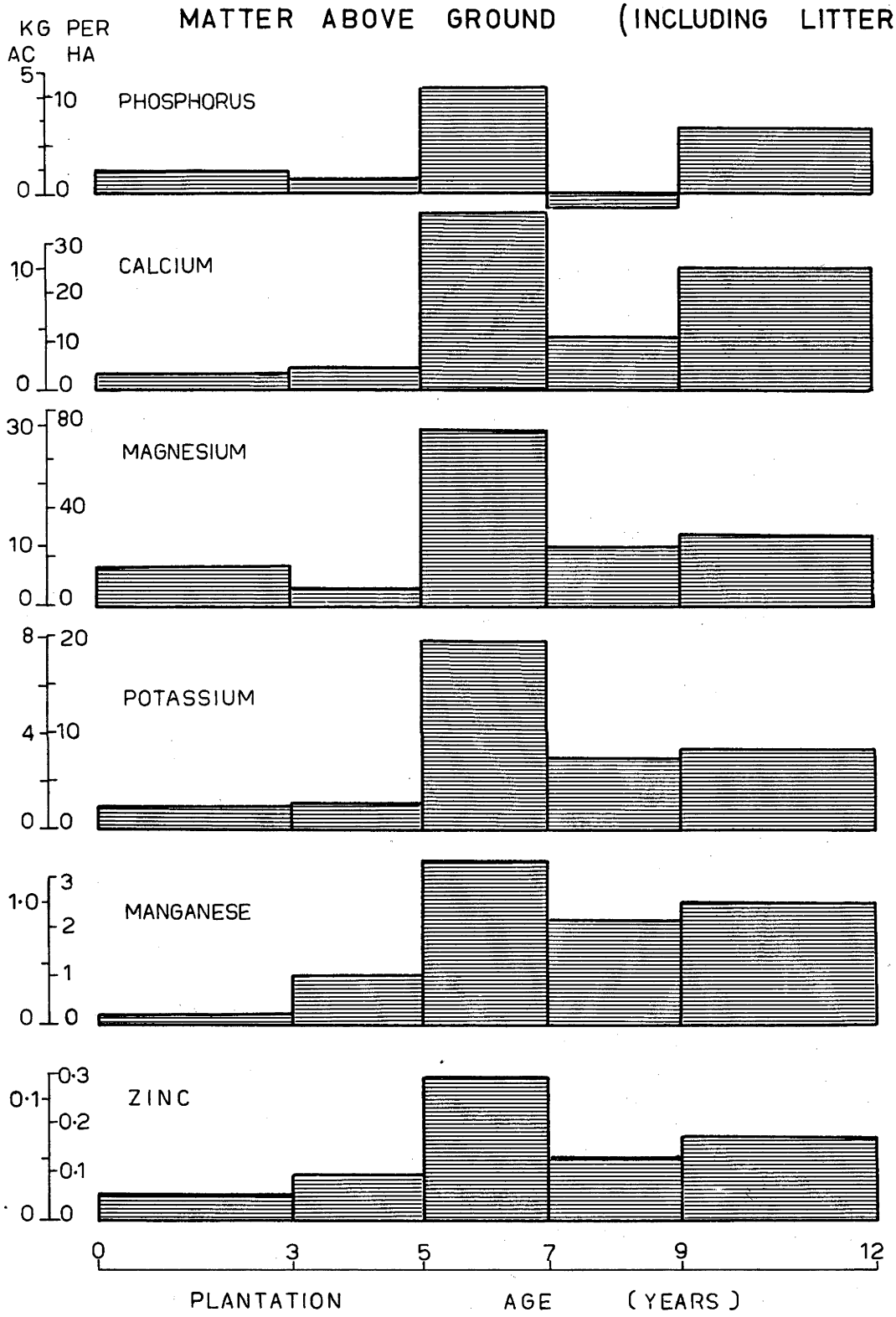
roots in the present study. However the oldest plot examined is far from maximum development.

The rate of nutrient accumulation has been calculated for many stands, but the results are difficult to compare because of lack of uniformity in methodology and in definition. For example, Cole et al.(1967) examined in detail the distribution of several minerals in a second growth Douglas fir ecosystem and evaluated the various nutrient transfer processes. The uptake of nutrients by forest vegetation was determined by sampling the current year's growth, special allowance was made for the continued accumulation of calcium in the foliage and branches after initial development but no similar allowance appears to have been made for a decrease in the nutrient content of older material which may influence total accumulation, particularly for phosphorus and potassium. Estimates of annual accumulation based only on current years growth probably would overestimate accumulation rates of some nutrients. The annual dry weight and nutrient accumulation in P. sylvestris plantations examined by Ovington (1959b) reached a maximum at about 20 years, but there was little evidence of a decline in nutrient uptake between then and 35 years. This pattern of nutrient uptake is probably repeated in many stands where initial development is relatively slow.

An important result from the present study is the difference between the maximum rates of nutrient accumulation during the period of maximum growth and the average rate of accumulation in older stands (Fig. 5.6).

The maximum rate of accumulation is 11, 38, 73, 19, 3.3 and 0.3 kg per ha per annum for the nutrients P, Ca, K, Mg, Mn and Zn respectively. A closer examination of nutrient redistribution within the stand is needed before the cycling of mineral nutrients through a pine stand can be more fully described.

FIG. 5-6 ANNUAL INCREASE IN THE MINERAL NUTRIENT CONTENT OF A P. RADIATA PLANTATION ORGANIC MATTER ABOVE GROUND (INCLUDING LITTER)



CHAPTER 6

SEASONAL CHANGES IN THE NUTRIENT CONTENT OF P. RADIATA FOLIAGE

Contents

CHAPTER 6

SEASONAL CHANGES IN THE NUTRIENT CONTENT OF P. RADIATA FOLIAGE

6.1 INTRODUCTION

The nutrient contents of several P. radiata stands have been determined (Chapter 5) and estimates made of nutrient accumulation and turnover through successive years. Seasonal variations in the concentrations and amounts of nutrients within the foliage may be substantial (Tamm, 1955). A marked decrease in concentrations and total amounts of most nutrients in the foliage with age occurred in the study plots; for example, in the oldest plots phosphorus concentrations decreased from 0.2% dry weight for 1- year old leaves at the tree apex to 0.1% for leaves, predominantly three years old, on the lowest branches. If the transfer of nutrients from older tissues is an important cause of the decrease in nutrient concentration, as has been suggested by Tamm (1955), Will (1966b) and Attiwill (1968), then such nutrients may contribute appreciably to the annual accumulation in new and actively growing tissues.

Olsen (1967) has commented "To demonstrate and interpret the relative importance of rates of internal circulation versus rates of import:export (as part of a larger scale geochemical cycle) is one of the unifying problems of cycling studies." Nutrient circulation within the plant may be as important in maintaining an adequate nutrient balance as circulation through the biomass.

Changes in nutrient contents of foliage with age, or the influence of litterfall on the cycling of nutrients cannot be determined adequately from data collected at a single

sampling of several stands. Consequently it was decided to study seasonal changes by taking leaf samples periodically through a full growing season from five trees in the 5- year old study plot and by collecting litterfall in both the 5- year and 12- year old plots. Details of the sample collection are given in Chapter 3, where the changes in leaf weight and amounts of litter fall are also discussed. In this chapter the nutrient contents of leaves on the tree and of litter are examined.

6.2 SEASONAL CHANGES IN FOLIAGE COMPOSITION

6.2.1 Methods

Samples of four leaf fascicles, each fascicle having three needles and the fascicle sheath removed, were collected in August, 1966. Samples were of 1-, 2-, and 3- year old leaves from five 5- year old P. radiata trees, and sampling was repeated through the year at about 6- week intervals (Chapter 3).

After oven-drying, each sample was digested and analysed for nutrient content following the methods described in Chapter 5.2. Thus both the concentration and total nutrient content in each sample of four fascicles were determined.

6.2.2 Results

Because the dry weight of leaves changes through the year, the nutrient concentrations expressed as a proportion of dry weight may be misleading in relation to nutrient movement. Total nutrient content is more appropriate and is used in this study.

The elements studied differ markedly in the pattern of increase or decrease with age (Table 6.1, Fig. 6.1). The amounts of phosphorus decreased steadily throughout the year for all leaves greater than 1- year old; the amount of potassium also decreased in each year but tended to remain

FIG. 6-1 CHANGES IN THE NUTRIENT CONTENT OF P. RADIATA LEAVES AS A PERCENTAGE OF THE CONTENT AT THE BEGINNING OF EACH YEAR

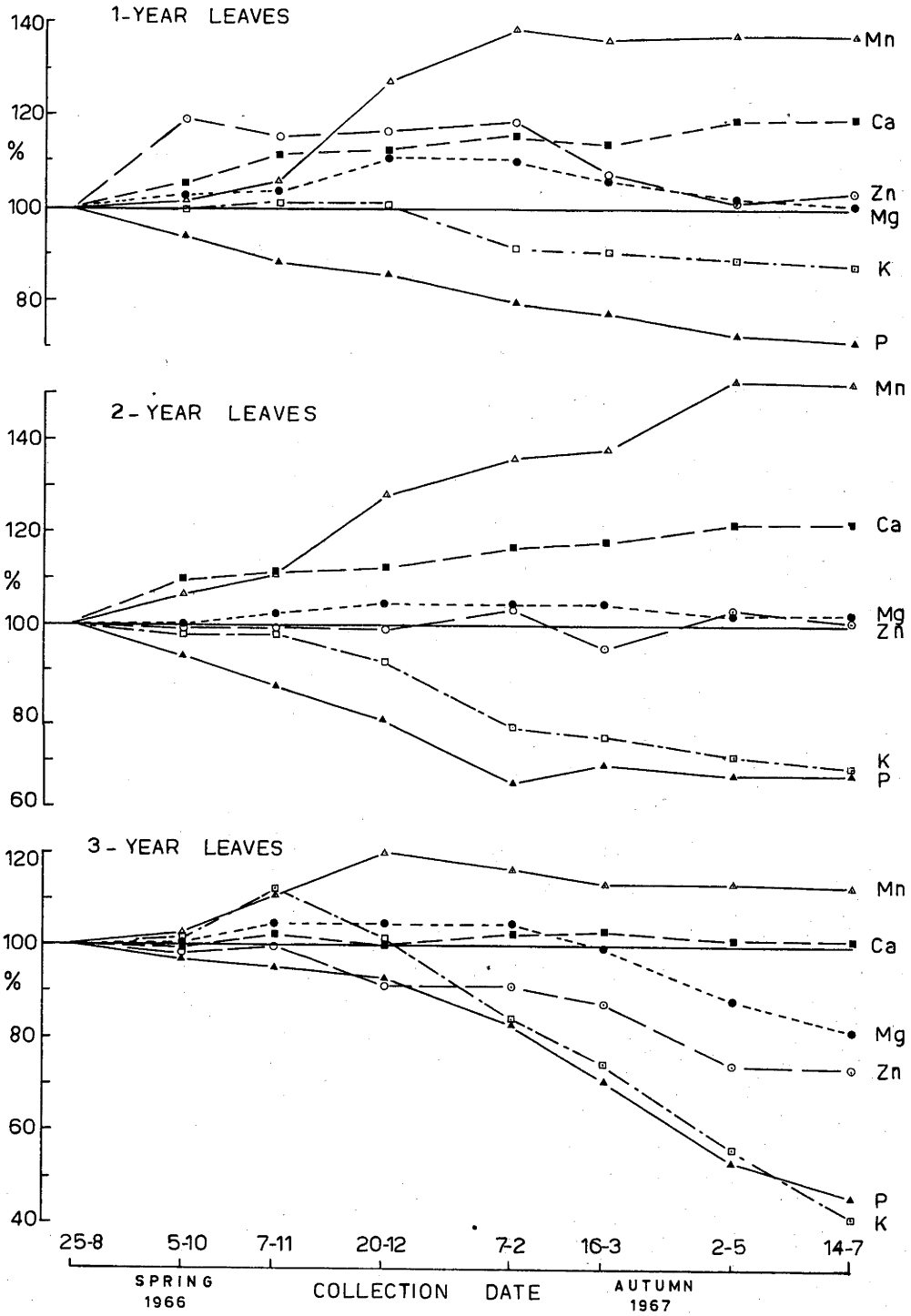


Table 6.1 Seasonal variation in nutrient content of P.radiata foliage
Amounts measured in four fascicles per collection
(Averages for five trees)

Nutrient	Year of Initial Growth	Collection date							
		25-8 1966	5-10 1966	7-11 1966	20-12 1966	7-2 1967	16-3 1967	2-5 1967	14-7 1967
Phosphorus	1965-66	0.67	0.62	0.57	0.53	0.50	0.48	0.44	0.43
	1964-65	0.41	0.37	0.34	0.30	0.23	0.25	0.24	0.24
(mg)	1963-64	0.32	0.31	0.30	0.29	0.25	0.20	0.13	0.10
Potassium	1956-66	3.48	3.47	3.54	3.51	3.11	3.06	3.00	2.95
	1964-65	1.83	1.78	1.78	1.63	1.32	1.26	1.16	1.12
(mg)	1963-64	1.19	1.20	1.37	1.21	0.93	0.80	0.53	0.30
Calcium	1965-66	0.82	0.87	0.94	0.95	0.98	0.96	1.01	1.02
	1964-65	0.66	0.74	0.75	0.76	0.80	0.81	0.84	0.85
(mg)	1963-64	0.79	0.78	0.81	0.79	0.82	0.82	0.80	0.80
Magnesium	1965-66	0.41	0.42	0.43	0.47	0.46	0.44	0.42	0.41
	1964-65	0.33	0.33	0.34	0.34	0.35	0.35	0.34	0.34
(mg)	1963-64	0.36	0.36	0.39	0.39	0.39	0.36	0.31	0.28
Manganese	1965-66	0.83	0.85	0.89	1.12	1.23	1.21	1.22	1.22
	1964-65	0.80	0.87	0.90	1.08	1.16	1.18	1.45	1.40
(gm x 10^{-4})	1963-64	1.12	1.16	1.28	1.40	1.35	1.30	1.32	1.30
Zinc	1965-66	10.3	12.7	12.3	12.5	12.7	11.3	10.6	10.8
	1964-65	10.5	10.3	10.4	10.4	11.0	10.0	11.0	10.7
(gm x 10^{-6})	1963-64	18.0	17.5	18.0	16.0	16.0	15.0	12.1	12.0

constant during the first few months of each growing season. However, no element shows substantial loss from leaves of any age early in the growing season as new growth commences.

Calcium and manganese increase steadily through the year in both 1- and 2- year old leaves, and either increase slightly (manganese) or remain nearly constant (calcium) in three year old leaves. Magnesium and zinc increase slightly early in the season in 1- year old leaves but remain constant thereafter until immediately prior to leaf abscission when the amounts of these elements decrease slightly.

6.2.3 Discussion

The results indicate a substantial decrease in phosphorus and potassium, and to a lesser extent magnesium and zinc after the young leaves are fully developed. This decrease is most marked prior to physiological death and abscission. The amounts of calcium and manganese continue to increase through the life of leaves (Table 6.1). If similar changes occur in older stands with closed canopy, as seems likely (Figs. 5.2a - f), the total weight change for each nutrient in leaves after the first year can be calculated (Table 6.2).

Table 6.2 Changes in the nutrient content of leaves in closed-canopy *P.radiata* stands (kg per ha per ann)

Nutrient	Total in foliage at end of season (Chapter 5)	Annual changes in leaves older than one year	Leached from total canopy (Table 6.3)
Phosphorus	14.3	-6.8	0.4
Calcium	26.1	+4.0	4.0
Potassium	68.5	-28.0	15.0
Magnesium	15.8	-1.0	2.0
Manganese	4.4	+0.6	
Zinc	0.34	-0.04	

TABLE 6.3 Summary of literature references to nutrient content of incident rainfall and removal of nutrients from foliage by rain

Reference		Species	Total rainfall cm/ann	Nutrient content of incident rain kg/ha/ann				Nutrients leached from vegetation kg/ha/ann				
				P	K	Ca	Mg	P	K	Ca	Mg	
Carlisle, et al. (1967)		Quercus	174	0.35	3.9	12.5	5.2	0.9	29.6	21.1	13.1	*
Madgwick and Ovington (1959)	(a)	Hardwoods	83		2.8	10.7	4.0		27.8	24.5	11.0	
	(b)	Conifers							22.6	24.1	8.8	
Duvigneaud and Denaeyer-De Smet (1967)		Oak-Birch	120		10.3	16.9			15.6	15.0		
Cole, et al. (1967)		Douglas fir		Trace	0.8	2.8		0.4	10.7	3.5		*
Attiwill (1966b)		Eucalypt	98		2.0	2.7	5.4		11.4	5.3	1.9	
Will (1959)	(B)	P.radiata		0.3	5.0	3.0		0.4	18.5	1.6		
	(C)	P.radiata	150	0.3	3.6	2.9		0.9	14.4	0.2		
	(F)	Douglas fir	170	0.5	8.6	3.7		3.7	16.5	1.7		
Miller (1961)			135	0.2	6.6	7.3	11.2					
Sviridova (1960) in Attiwill (1966b)	(a)	Hardwood						0.2	2.7	5.5	1.1	
	(b)	Pine						trace	1.0	6.0	0.9	
Estimated for closed canopy P.radiata				0.25	3.0	3.0	4.0	0.4	15.0	4.0	2.0	

* Leachate includes stemflow

A broad estimate of the amounts of nutrients leached from a closed canopy P. radiata stand can be obtained from the results of studies in many diverse forests (Table 6.3) to determine whether leaching is a significant cause of nutrient loss. Since the reported results are generally similar, the estimates are probably reasonably accurate.

Only 6% of the decrease in foliar phosphorus can be attributed to leaching; the calcium content of foliage increases with age despite appreciable leaching, and more magnesium is leached than the net loss from foliage over 1- year old. The estimates of nutrient decrease in leaves through leaching probably overestimate because losses from leaves younger than 1- year old and branch wood are not included and no allowance is made for dust and aerosols washed from the canopy by rain (Carlisle, et al., 1967; Attiwill, 1966b). Furthermore, Tukey and Mecklenburg (1964) have shown radioactive calcium, phosphorus and strontium absorbed through the roots may be leached from foliage, reabsorbed and returned to the foliage relatively quickly. The total amount of each element estimated as washed from the tree crown (Table 6.2) would be obtained if on each of only 10 rain occasions through a year 0.4%, 1.5%, 2.2% and 1.2% of the foliar phosphorus, calcium, potassium and magnesium respectively, were leached from the crown, and presumably these amounts could be both leached and replaced readily. Thus, whilst the amounts of nutrients estimated as leached from vegetation contribute to overall circulation, leaching of foliage by rain seems of minor importance as a cause of decrease of foliar nutrients. No other external reasons for nutrient decrease were obvious in the study area, but sapsucking organisms such as aphids might have been effective even though these were not observed. The leaves on the study trees showed no evidence of damage during the second and third year on the tree, and few, if any, leaves were removed or shed before the fourth year.

During the fourth year leaves died progressively along each branch from the bole so the sample population changed and sampling bias could have occurred, but only during the final months when there was little difference in nutrient content between leaves shed and those remaining on the branch (Chapter 6.3).

Consequently, for those nutrients showing a decrease in total content per leaf after initial development, most of this decrease must be attributed to internal redistribution within the tree, and possibly the nutrients are then available for utilization at other actively growing centres. The redistribution of some nutrients within the plant during normal development, particularly from the older, metabolically less active cells to younger, more active cells has been widely accepted, and nutrients are commonly classified as mobile (e.g. phosphorus and potassium) or immobile (e.g. calcium) depending on the degree of redistribution (Nason and McElroy, 1963; Hewitt, 1963).

The direction and amount of movement of a particular nutrient at any time probably results from a complex interaction between factors such as net availability to the plant and concentration in the translocation stream, rate of removal into other growth zones, metabolic and physiological function of the nutrient and its solubility. The importance of redistribution is illustrated for phosphorus; after canopy closure when new leaf growth is balanced by shedding of older leaves, then in any year all but 10 - 15% of the phosphorus accumulated by new foliage growth might be supplied by recirculation from the older foliage (Table 6.4). The accumulation of manganese and calcium in the new foliage is met mainly from other sources than the older foliage. Probably the proportion of nutrients redistributed increases as the concentration gradient within the translocation stream increases, as a result of more rapid tree development or reduced nutrient supply from the soil. If so, such an

increase in movement from older leaves would explain the variable pattern of zinc concentrations in the foliage between young and older, rapidly expanding trees (Fig. 5.2).

TABLE 6.4 Changes in the nutrient content of *P. radiata* foliage as a percentage of content in 1-year old leaves

Nutrient	Weight accumulated in first year	Percentage change in content from 1st year				
		2nd year	3rd year	to leaf fall	Total loss	Total increase
Phosphorus	100	-40	-25	-25	90%	
Potassium	100	-15	-30	-40	85%	
Calcium	100	+20	+35	nil		55%
Magnesium	100	nil	nil	-20	20%	
Manganese	100	+45	+110	+45		200%
Zinc	100	+ 5	nil	-30	25%	

6.2.4 Summary

Whilst recognising the limitations of the data obtained in this study, some tentative conclusions seem justifiable:

(1) The most mobile nutrients, phosphorus and potassium, are able to re-enter the translocation stream after a period of initial rapid accumulation in young leaves. After the first year of leaf growth the amounts of both nutrients decrease, slowly during the second year and then more quickly, so that when leaves are shed in the fourth year only 10 - 20% of the 1st- year content remains.

(2) Calcium and manganese accumulate progressively during the first three years and there is little or no withdrawal of these elements before the leaves die.

(3) The amounts of zinc and magnesium in leaves remain more or less constant after the first year until immediately prior to leaf fall when the amount decreases by 20 - 40%.

(4) There was no evidence of a marked seasonal influence on the movement of nutrients; the pattern of increase or decrease was usually more or less uniform through the year, although potassium contents usually remained constant during the period of active growth (August - November) and decreased substantially after mid-summer.

(5) In order to characterize mineral nutrient cycles more adequately, more substantial data are required of:

i. the changes occurring in leaf structure and composition with increasing tree age, particularly during the period to canopy closure,
ii. changes in leaf composition over the full leaf cycle, including the critical first year of leaf development, and particularly the effect of site variation on nutrient translocation, and
iii. the role of other components, for example bole wood, in the internal redistribution of nutrients.

Whilst these facets could not be studied adequately because of time limitations, the broad pattern obtained of nutrient mobility provides a basis for further, more intensive study.

6.3 NUTRIENT CONTENT OF LITTER FALL

6.3.1 Methods

Leaf and male cone litter fall was collected at about 6 - week intervals for 12 - months from two study plots, No. 4, i.e. 5 - years old and No. 1, i.e. 12 years old (Chapter 3). After oven-drying, samples were taken for chemical analysis of leaf and male cone material from each of the five litter frames per plot. The analytical procedures used were as described previously (Chapter 5).

6.3.2 Results and Discussion

The concentrations of mineral nutrients in the *P. radiata* leaf litter varied during the twelve months, but

only relatively slightly as compared with the variation within the younger leaves in the tree crown. This variation did not occur systematically with the season, and generally each nutrient was present at a similar level to that in the oldest dead leaves on the trees (Table 6.5). Occasionally a small proportion of fresh leaves blown from the tree crown caused some variation in average composition, and during the spring there was some contamination of leaves by pollen (the pollen also is a form of litter), but the effects of these influences cannot be measured. The weights of nutrients returned to the forest floor in litter in the two stands are listed in Table 6.6.

Table 6.5 Concentration of nutrient elements in litter fall from *P. radiata* stands

Nutrient		Concentration in foliage. Range during year	Concentration in male cones	
			Before pollen shed	After pollen shed
Plot 1 (12 years)				
Phosphorus	% dry wt.	0.08 - 0.13	0.20	0.06
Calcium	% dry wt.	0.34 - 0.46	0.06	0.11
Potassium	% dry wt.	0.34 - 0.55	0.50	0.07
Magnesium	% dry wt.	0.12 - 0.15	0.13	0.14
Manganese	ppm	285 - 470	100	140
Zinc	ppm	21 - 30	29	30
Plot 4 (5 years)				
Phosphorus	% dry wt.	0.05 - 0.11	0.25	0.05
Calcium	% dry wt.	0.26 - 0.55	0.07	0.15
Potassium	% dry wt.	0.31 - 0.47	0.68	0.05
Magnesium	% dry wt.	0.10 - 0.13	0.13	0.08
Manganese	ppm	250 - 410	65	140
Zinc	ppm	38 - 53	30	47

Table 6.6 Nutrient content of annual litter fall in *P. radiata* plantations

Nutrient element	Weight in annual fall of Leaves	Male cones (kg per ha)	Total	Confidence limits of Total (P=0.05)	Male cones as percent of total
Plot 1 12 years					
Phosphorus	4.1	0.4	4.5	0.7	8.9
Calcium	16.2	0.5	16.7	3.2	3.0
Potassium	16.7	0.7	17.4	2.1	4.0
Magnesium	5.45	0.60	6.05	0.54	9.9
Manganese	1.45	0.06	1.51	0.28	4.0
Zinc	0.12	0.01	0.13	0.02	7.7
Plot 4 5 years					
Phosphorus	0.177	0.018	0.195	0.078	9.2
Calcium	0.730	0.030	0.760	0.300	3.9
Potassium	0.760	0.040	0.805	0.380	5.0
Magnesium	0.225	0.025	0.250	0.091	10.0
Manganese	0.060	0.003	0.063	0.028	4.8
Zinc	0.009	0.001	0.009	0.003	9.0

Male cones were not collected from the sample trees, but early in the spring many entire mature male cones were collected as litter. The concentrations of most nutrients in this material was similar to the concentrations in young leaves (Table 6.5) although calcium (0.06%) and manganese (60 - 100 ppm) were substantially less. Later in the season the male cones collected as litter were open, dry and empty of pollen and the average concentration of some nutrients was markedly different; phosphorus and potassium had decreased substantially, calcium and manganese concentrations increased, while magnesium and zinc remained more or less constant. However, the dry weight of the male cones also decreased during the collection period due to pollen shed and respiration.

The litter collected from the two plots differed little in composition, except for zinc and magnesium where the variation between plots in both leaves and male cones was similar to the variation in the sample trees (Chapter 5).

The weight of each nutrient element in the litter fall during the year in the 5- year old stand is only a small proportion of the total amounts accumulated in the P. radiata trees that year; for example, about 1% for phosphorus and 2% for calcium. In older stands turnover of nutrients through litter fall and decomposition may be an important part of the nutrient cycle (Table 6.7). The total amount

Table 6.7 Rate of nutrient turnover in P. radiata stands as a proportion of total annual accumulation after canopy closure

Nutrient element	Net accumulation per annum (kg per ha)	Total in litter fall (kg per ha)	Approx total accumulation (kg per ha)	Nutrients in litter as % of total accumulation
Phosphorus	4.7	4.5	9.2	48.9
Calcium	17.5	16.7	34.2	48.8
Potassium	25.0	17.4	42.4	41.0
Magnesium	6.9	6.1	13.0	46.9
Manganese	0.75	1.51	2.26	66.8
Zinc	0.20	0.13	0.33	39.4

of each nutrient accumulated by the pine stand each year is equal to the net accumulation (as calculated in Chapter 5) together with the amounts falling in litter and other losses. While the canopy is increasing, nutrients in litter fall are a small proportion of total accumulation, but after canopy closure the proportion increases and the cycling of nutrients becomes effective, unless the decomposition of fallen litter is slow.

The dry weight of litter collected in the 12- year old stand was greater than expected in view of the total crown weight (Chapter 3.3.2). Consequently the amounts of nutrients falling in litter may be greater than for an average year after canopy closure. However the estimated net accumulation rate probably over-estimates uptake after canopy closure because of the pruning in the 8th year after which foliage weights increased, and in later years the accumulation

of nutrients in the bole wood may decrease. Total nutrient uptake may also be underestimated due to pollen blowing from the stand but the total loss is probably relatively small, even though the concentration of some nutrients in pollen may be large. Whilst the nutrient amounts calculated for both accumulation and turnover after canopy closure are necessarily approximate and may vary from year to year and with tree age, the weight of each nutrient returned to the forest floor is a substantial proportion of the total uptake by the trees during the year (Table 6.7).

Thus the rate of breakdown and decomposition of the litter layers may become a critical limiting factor in the maintenance of an efficient nutrient cycle.

6.3.3 Summary

(i) While plantations of P. radiata are young and the crowns of individual trees are expanding litter fall is small, both in total and when compared with total organic production. Consequently, the rapid uptake and accumulation of mineral nutrients within a stand must be met almost completely from the soil system, although the death and decomposition of the understory vegetation may provide some nutrients.

(ii) After canopy closure, nutrients accumulate in the growing bole and branch wood components and also in the foliage to replace the amount lost in litter fall. In the older study plots the nutrients contained in litter fall amounted to about half the total uptake per annum.

(iii) Most of the annual turnover of mineral nutrients is through leaf litter fall. The death and turnover of branchwood appeared unimportant in this study because the lowest branches had been pruned from the older trees. However, the progressive death and decomposition of branches may add to the amounts of nutrients cycling through litter.

(iv) The amounts of nutrients returned to the forest floor in male cone parts varied from 3 - 5% (for calcium, potassium and manganese) to nearly 10% (for phosphorus, magnesium and zinc) of the total annual return, but would be greater in years of heavier male cone production.

(v) Little change occurs through the year in the chemical composition of falling litter, so the amounts of each nutrient returned from the tree during the year follow closely the pattern of dry weight litter fall, i.e. maxima during the spring - early summer and late autumn - early winter, but the proportion falling in the two main periods probably varies between localities. The slight seasonal distribution of nutrient return in litter probably has little effect on the rate of release to the soil.

CHAPTER 7

CONCLUSIONS. NUTRIENT ACCUMULATION AND CIRCULATION IN A RADIATA PINE PLANTATION ECOSYSTEM

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CHAPTER 7

CONCLUSIONS. NUTRIENT ACCUMULATION AND CIRCULATION IN A RADIATA PINE PLANTATION ECOSYSTEM

7.1 EXTERNAL INFLUENCES ON THE NUTRIENT CYCLE

The amounts and distributions of nutrients within a forest ecosystem may be changed by many factors which impinge on the system from time to time. The removal of forest produce, fires, animal consumption of plant material and leaching in drainage water may be important causes of nutrient loss. Pruning, thinning and the decomposition of dead organic matter substantially alter the nutrient distribution pattern, whilst the amounts of nutrients within an ecosystem may be increased by applied fertilizers, dust, rainfall, soil weathering and animal activity.

The original eucalypt forest of the study area had been logged and burnt, but during the first twelve years after the pine plantations were established there had been no thinning, crop removal, fires or fertilizer addition. Woody regrowth was cut down to reduce competition with the pines, and the grasses and low vegetation had been grazed, mainly by rabbits. These influences cause some redistribution of minerals within the ecosystem as does pruning and litter decomposition, but all may be regarded as internal to the ecosystem.

Because of shortage of time, no measurements were made from which the amounts of nutrients entering or leaving the study plots could be estimated accurately. However, from numerous other studies nutrients added in rainfall and dust are known to be of greatest importance. These additions can be estimated with reasonable accuracy from the published

data which give fairly similar results (Table 6.3). These estimates may be compared with data already presented to assess the relative importance of the several pathways within the nutrient cycle of the plantation ecosystem.

7.2 PATHWAYS IN THE NUTRIENT CYCLE

The movement of mineral nutrients within a forest plantation can be illustrated schematically to aid assessment of total and periodic movement from the soil to the vegetation and the relative importance of the various pathways in the total nutrient cycle (Fig. 7.1). As examples, estimates have been prepared of the movement and distribution of phosphorus, calcium and potassium at three contrasting stages of plantation development, i.e. before, during and after canopy closure (Table 7.1). All available data have been taken into account in the compilation of the table so the overall pattern is probably realistic, although individual values vary in precision and estimates are restricted to above-ground movement of nutrients because of limited data for plant roots. The relative importance of the various pathways at each successive plantation phase can readily be distinguished.

Of the total amount of each nutrient accumulated into the trees each year only a small proportion is in male cones and even less is lost as pollen from the forest stand. In contrast, appreciable amounts of some nutrients are leached from the foliage and other above-ground plant parts by rain, this is particularly important where such nutrients tend to be lost from the site in drainage water or fixed within the soil. About 30% of the total potassium uptake after 12 years may be to replace potassium leached from the trees and possibly subsequently leached from the site.

Most of the total phosphorus and potassium uptake by trees in a plantation in any year accumulate in the new growth. A substantial amount of calcium is deposited in

Fig. 7.1 Diagramatic representation of the important pathways for mineral nutrient movement in a pine plantation ecosystem

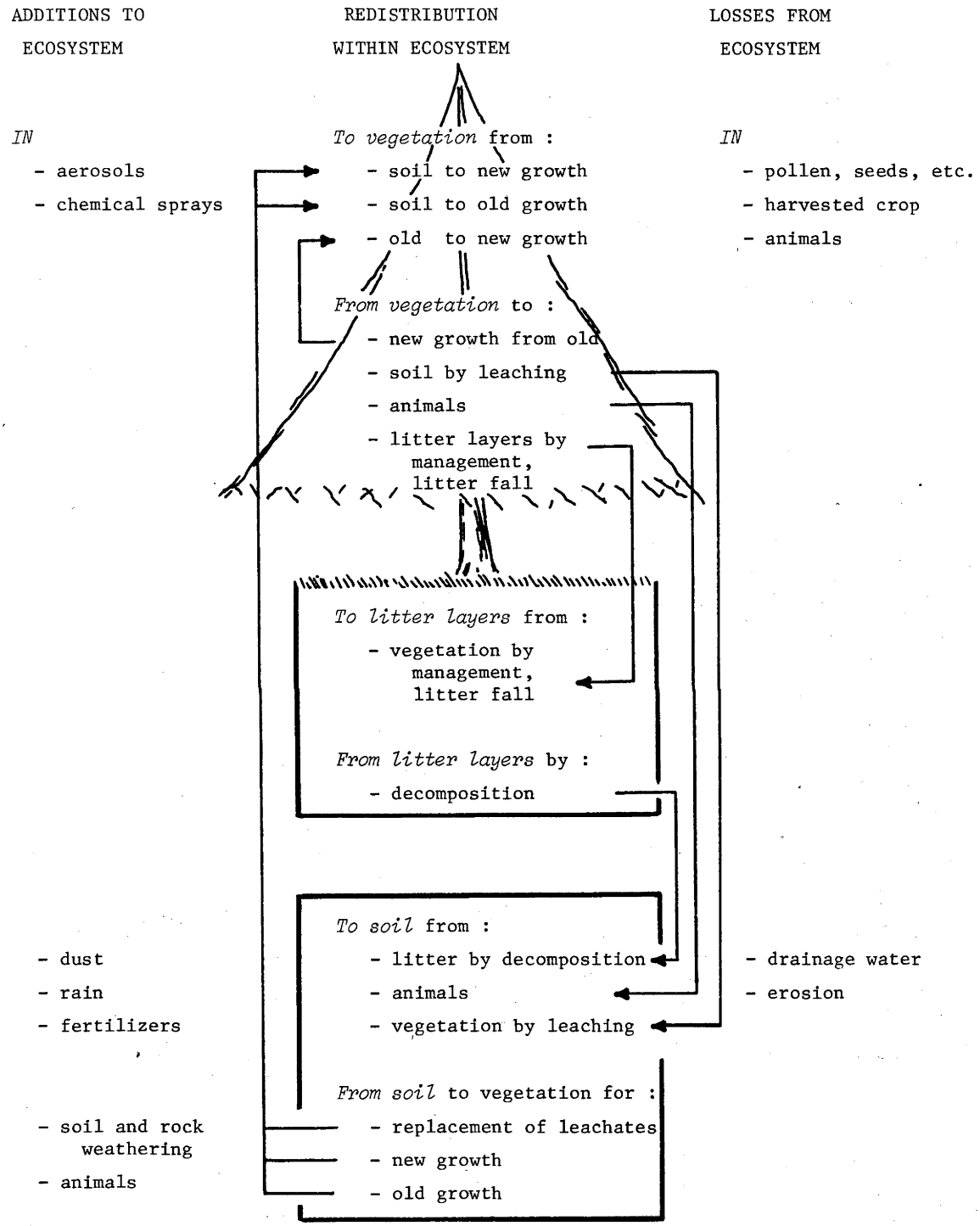


Table 7.1 Estimates of nutrient movement along pathways in the nutrient cycle of a *P. radiata* plantation (kg per ha per annum)

Pathway of nutrient movement	Age 4-5 yrs			Age 6-7 yrs			Age 12-13 yrs		
	P	Ca	K	P	Ca	K	P	Ca	K
Additions to ecosystem:									
Dust, rainfall, etc.	0.3	3.0	3.0	0.3	3.0	3.0	0.3	3.0	3.0
Fertilizers		-----		---	nil	---		-----	
Soil weathering, animals		-----		-- not known		---		-----	
Losses from ecosystem:									
Pollen, seeds, etc.		-----		-- negligible		--		-----	
Harvesting erosion		-----		---	nil	---		-----	
Animals, Drainage		-----		-- not known		---		-----	
Redistribution within ecosystem									
Soil to new growth	2.1	3.6	8.5	15.0	51.0	135.0	8.5	13.7	37.5
Soil to old growth	-	1.0	-	-	9.0	-	-	15.0	-
Old to new growth	1.0	-	4.0	5.0	-	15.0	15.0	-	75.0
Leaching from canopy	0.1	0.8	3.0	0.3	3.0	12.0	0.4	4.0	15.0
Litter fall	0.1	0.6	0.5	3.0	15.0	15.0	4.5	16.7	17.4
Decomposition of litter	0.1	0.1	0.5	2.5	12.0	10.0	4.5	8.7	17.4
Totals									
Soil to plants (including replacement of leachate)	2.2	5.4	11.5	15.3	63.0	147.0	8.9	32.7	52.5
Additions to soil reserve	0.5	3.9	6.5	3.1	18.0	25.0	5.2	15.7	35.4
Uptake from soil reserve	1.7	1.5	5.0	12.2	45.0	122.0	3.7	17.0	17.1
Totals contained at beginning of period (kg per ha)									
in pine trees	2.0	4.0	12.5	14.0	30.0	70.0	35.0	105.0	310.0
in other vegetation	6.2	7.5	42.0	4.0	6.0	23.5	0.5	1.0	1.0
in litter	1.0	5.5	2.5	3.0	12.5	7.5	15.5	90.0	40.0
in biomass	9.2	17.0	57.0	21.0	48.5	101.0	51.0	196.0	351.0

older tissues, for example after canopy closure the increase in calcium in older tissues is similar to that accumulated in the current year's growth. The internal redistribution of mobile nutrients, particularly potassium and phosphorus, may be important for an adequate supply of those nutrients to the new growth at all stages of stand development; after canopy closure, redistribution from older tissues may exceed uptake from the soil. Appreciable quantities of most nutrients are cycled through the litter. The rate of litter breakdown and consequent nutrient release is an important factor in total nutrient availability, particularly for nutrients such as calcium which are not substantially redistributed internally before leaf fall.

The amounts of each nutrient added to the ecosystem in dust, rainfall, etc., vary between localities and with time, and the proportions retained by the ecosystem also vary. The available data indicate additions of phosphorus are small, but the amounts of other elements added in precipitation may be important to the total reserves, particularly during the early establishment years and again after canopy closure.

The schematic representation of nutrient movement (Figure 7.1) indicates likely sources of error in the various estimates of stand nutrient content and rate of accumulation made either by one or successive examinations within a stand or, as in this study, by comparison of stands over an age series. Reference has been made to the study by Cole, et. al., (1967) in which the rate of nutrient accumulation was calculated from only the current years growth (Chapter 5.5). Data in Table 7.1 indicate for the older P. radiata stands more than half of the annual accumulation of some nutrients into new growth comes not from the soil but from older tissues, so estimates of uptake based on current growth alone may overestimate the rate of uptake by more than 100%. Cole, et al. discussed the nutrient transfer processes (i) from the soil to the tree, (ii) of return

from the tree to the forest floor, and (iii) leaching from the forest floor to the soil, but possibly drew incorrect comparisons between them by failing to consider the internal redistribution processes. For some nutrients, particularly phosphorus, transfer within the tree may be greater than any of the previous three processes.

7.3 RELEVANCE OF THE STUDY TO FOREST SILVICULTURE

The broad pattern of accumulation shown for all mineral nutrients is closely related to the pattern of dry weight increase, i.e. slow accumulation during an establishment period of several years, then very rapid increase over a short period to canopy closure and finally a nearly constant rate of accumulation at less than the maximum rate after canopy closure. When nutrient availability, uptake and circulation are taken into account, important differences from the pattern of organic production and decomposition are evident and must be considered when the growth or potential growth of a plantation is studied.

The importance of these differences in relation to nutrient requirements for P. radiata stands, and in stands of different ages, in determining future growth and response to fertilizer addition on deficient sites can be illustrated by considering several contrasting field situations.

(i) Phosphorus deficiency

Phosphorus deficiency symptoms have been observed in many pine plantations in Australia, in some areas the total soil phosphorus resource is small; elsewhere the total soil phosphorus resource may be considerable but the rate of availability is small due to extreme fixation within the soil system (e.g. Baur, 1959). When the rate of phosphorus availability is small but relatively uniform during the period of a pine rotation, the initial growth of pine seedlings may be rapid; but before full crown development is achieved the potential phosphorus uptake may exceed

availability and growth would then be abruptly reduced. Additions of phosphorus in rainfall are small but internal and external circulation of phosphorus is rapid, so growth may continue slowly, determined by the rate of phosphorus availability. Under these conditions fertilizer addition at the time of planting has little effect but later applications may avert the decline in growth rate. Phosphorus released from organic matter may be continually fixed into the soil clay system and so the overall availability would remain low, or phosphorus addition may be required only to satisfy the maximum rate of requirement immediately at canopy closure, after which the lesser rate of requirement may be supplied from the soil.

(ii) Potassium deficiency

The growth of pine trees is sometimes limited by an inadequate supply of potassium in the soil (Hall and Purnell, 1961). Usually growth is depressed soon after planting, but on some sites the deficiency is not extreme and the trees continue to grow slowly. Native grasses and other vegetation with a high potassium content compete strongly during the establishment years, but as the tree crowns slowly develop the other vegetation may become a source of potassium for the trees. Additions in rainfall may increase the total potassium resource as the mass of organic matter increases, and redistribution within the trees and through litter is rapid, so growth may continue and even improve as more potassium is incorporated within the biomass.

(iii) Calcium deficiency

Calcium deficiency has not been widely reported for Australian plantations but there is some evidence of growth limitations in older plantations due to inadequate soil calcium (Humphreys, 1965; Humphreys and Gentle, 1968).

Apparently for most plantations, initial calcium requirements, including the maximum rate of accumulation at

canopy closure, can be supplied from the soil. Later in the rotation, the balance between soil availability and plant requirement may alter as a substantial proportion of the initial soil resource is accumulated within the tree and litter layers. Gains to the ecosystem from rainfall may be appreciable, but redistribution through litter fall is slow and calcium continues to accumulate in both old and young tissues. Consequently, as the total amount of calcium accumulated increases the growth of trees may be progressively reduced.

The addition of calcium in fertilizers would probably have little effect under these conditions until the total requirement exceeded the soil resource, which may be late in the rotation.

The above illustrations indicate the many factors that have to be considered before the results of fertilizer experiments and the growth of young plantations can be fully assessed and extrapolated to predict future growth. Apart from the total soil resource and the availability of each essential nutrient element, future tree growth may be influenced by the degree of stand development, litter fall and decomposition, the degree of internal nutrient redistribution, the amounts of each nutrient added from external sources and the amounts lost from the ecosystem or made unavailable within the system. The production rate of a forest stand may be improved or maintained by nutrient addition, but only to a level defined by the many other environmental factors.

7.4 LIMITATIONS OF THE STUDY

From the data presented in Part II, the important changes in the accumulation and distribution of several mineral nutrients within a P. radiata plantation can be described. The main limitations in using these data result from the restrictions of the study in both space and time.

Firstly, the changes described are those occurring above ground. Roots commonly are equivalent to about 20% of the total above-ground biomass (Chapter 2), and the concentrations of most nutrients are generally of a similar order in the roots as in the branch wood (Cole, et al., 1967; Ovington and Madgwick, 1959 b; Young and Carpenter, 1967). This concentration is close to the overall average in young trees and consequently the rate of nutrient accumulation in the total biomass is probably underestimated by about 20% during the early years of maximum accumulation when only the above ground parts are taken into account. Data are required of the total amounts of nutrients accumulated within the root systems of trees under varying conditions, and also of the turnover of nutrients through the roots as a result of seasonal changes in root mass. Accurate data for the dry weight of roots are difficult to collect and it is even more difficult to estimate their nutrient content.

The pattern of nutrient distribution is also affected by the environment and by management. For example, total growth, the distribution of growth and the rate of turnover through litter fall and decomposition may all vary according to initial stocking density and fertilizer additions, or because of differences in water availability (e.g. Kramer, 1959). The effects of these factors on nutrient accumulation and movement need closer study.

The importance of redistribution of nutrients within the tree as a factor in the overall nutrient cycle has been shown. Data were gathered from several sources with varying reliability so internal redistribution could be estimated, and possibly some of the nutrient decrease in leaves was due to factors not assessed in this study; nevertheless, the relative magnitudes of the various data are probably reliable. The redistribution of nutrients between older and young tissues of other components may also be important, for example the central heart wood of the bole frequently has a smaller

concentration of the mobile nutrients than the outer sapwood. Whilst the changes in nutrient concentrations across the bole may be due to several factors, any difference is probably related to the decrease in physiological activity of woody tissues with age. The processes of nutrient redistribution from all tissues and the effects of external factors, as soil nutrient status, on redistribution require further examination.

The physical and chemical measurements made of trees in the five study plots indicate the plots depict closely the growth of a single stand. However, more complete data of many processes could be obtained from studies of longer duration through a pine rotation.

Finally, although the study plots appeared to have relatively uniform soil and environmental conditions, the trees of each plot varied considerably in total dry weight, the distribution of dry weight between components and in nutrient content. Variations of this kind have important sampling implications for studies of total growth and also for the assessment of site fertility and of responses to fertilization. The differing rates of nutrient accumulation between apparently similar trees may significantly influence the results of tree improvement selections, but there are few data to indicate the relative importance of small changes in environment or differences in tree genotype as factors contributing to the overall variation observed. Consequently it was thought desirable that this aspect of the study be considered in greater detail.

PART III

BETWEEN - TREE VARIATION IN NUTRIENT CONTENT OF *PINUS RADIATA* TREES

CHAPTER 8

PHENOTYPIC AND GENOTYPIC VARIATION IN THE NUTRIENT CONTENT OF P. RADIATA PLANTATION TREES

CHAPTER 8

PHENOTYPIC AND GENOTYPIC VARIATION IN THE NUTRIENT CONTENT OF P. RADIATA PLANTATION TREES

8.1 INTRODUCTION

The nutrient content of trees examined in plots of the age series (Chapter 5) were generally closely related to the tree bole size, so highly significant relationships between nutrient content and bole size could be calculated. Although the average concentration of nutrients varied between trees this was very much less than the variation in total dry weight, so small trees contained less nutrients than large trees in nearly the same proportion as their weights. However, the data also showed individual trees of similar size may differ substantially in their component distributions of dry weight and in the total amounts of nutrients contained.

Trees with similar bole volumes or with similar total dry weight may have markedly different crown weights; also, the concentrations of nutrients in comparable tissues may vary from tree to tree, so the quantity of nutrients accumulated by similar trees may differ by about 30% (Table 8.1). Only part of the nutrients accumulated by a tree may be essential for the level of growth obtained, and the excess represents luxury uptake. Differences in nutrient content may then reflect only a variable supply of excess nutrients. However, wide variation in nutrient content may occur when the availability of that nutrient is limiting tree growth; this could also result from variable nutrient supply, but might indicate differences between trees in their ability to absorb and utilise nutrients.

TABLE 8.1 Examples of between - tree variation in nutrient content in a *P. radiata* stand. Dry weights and nutrient contents of small, average and large trees sampled in study plot 3 (7 years) Billapaloola Plantation (Chapter 5)

Sample tree number	1	3	5	4	9
Bole diameter (cm)	6.4	9.6	10.9	10.6	14.5
Bole volume (cu m)	0.020	0.048	0.071	0.076	0.134
Total canopy					
Dry weight (kg)	2.68	11.85	12.79	11.71	31.93
Weight phosphorus (gm)	3.24	10.56	11.77	10.83	25.98
Weight calcium (gm)	5.52	26.92	36.72	26.51	82.91
Weight potassium (gm)	17.98	70.82	68.23	65.67	171.54
Total tree					
Dry weight (kg)	6.88	20.94	26.50	24.37	55.85
Weight phosphorus (gm)	4.13	12.83	14.25	13.51	31.94
Weight calcium (gm)	7.86	31.46	42.62	33.19	93.17
Weight potassium (gm)	28.51	98.65	98.84	97.42	242.76

Within-species variation in nutrient content and in reaction to nutrient stress has been demonstrated for many agronomic plants, for example in Trifolium and Festuca species (Snaydon and Bradshaw, 1961, 1962; Snaydon, 1962). Epstein and Jefferies (1964) have discussed the between-plant differences in nutrient content for a wide range of agricultural and pomological crop species, and reviewed the evidence for selective ion translocation. Steinbeck (1966) has pointed out small differences in the ability of individual trees to accumulate nutrients may make the difference between stagnation and growth of plantations and Gerloff (1963) has discussed some of the ecological implications of small variations in nutrient requirement within and between species. The large differences in the nutrient content of adjacent trees or in growth observed in P. radiata plantations of low nutrient status are unlikely to be caused only by minor and local variation in site. The possibility and likely significance of a genetic basis for variation in nutrient content and utilization in P. radiata requires investigation.

Many studies into within-species nutrient requirement have been made for species with wide geographic or edaphic provenance; such studies with tree species have usually been made by assessing the variation in foliar nutrient concentrations, or by comparing growth responses of seedlings for several provenances of the species to particular soils or growth media. For example, significant differences have been observed in the foliar nutrient concentrations between various provenances of Scotch pine (Gerhold, 1959; Steinbeck, 1966); differences in uptake and distribution of phosphorus between seedlings of several slash pine progeny groups were reported by Walker and Hatcher (1965), and the growth responses to fertilizer addition also varied between groups. Similar variation in growth and nutrient uptake has been reported for provenances of Norway spruce (Giertych and Fober, 1967), clones of Populus deltoides (Curlin, 1967) and provenances of Jack pine (Mergen and Worrall, 1965).

Snaydon (1962) observed that when the progeny of natural populations of Trifolium species from contrasting soil types were grown in pot culture each population performed best in its native soil; the natural populations were described as "edaphic ecotypes". Similar variation in response to substrate by seedlings has been demonstrated for numerous native plants, e.g. strains of Streptanthus glandulosus from either serpentine or non-serpentine soils show a marked intolerance for the alternate soil (Kruckeberg, 1951); also seedlings of several provenances of Eucalyptus cladocalyx varied in response to changing substrate nitrogen and phosphorus (Groves, 1967), and the response differences were attributed to differences in ability to absorb nutrients from solutions at low concentrations.

Fielding and Brown (1961) have reported genetic variation in the reaction of P. radiata to nutrient stress under field conditions, although it is difficult in that study to differentiate between variation in natural vigour (e.g. photosynthetic capacity and net assimilation), reaction to nutrient stress and reaction to other environmental limitations (particularly to water stress).

The natural range of P. radiata is limited to about 40,000 ha (16,000 ac), where the soils are mainly derived from shallow marine deposits overlying various volcanic and sedimentary country rocks (Roy, 1966). Whilst P. radiata provenances have been recognised, probably most plantations in Australia have originated from the Monterey stands where the edaphic range is small (Fielding, 1961; Roy, 1966). Consequently it is less likely that edaphic ecotypes or between-provenance variation in nutrient status, similar to those reported for geographically widespread plants, would be important in Australian plantations. Variation in nutrient status between trees within a P. radiata plantation more likely results from physiological and morphological diversity naturally present in the wild parent population.

Much of the diversity between trees in total nutrient content can be attributed to contrasting weight distribution, particularly to differing amounts of foliage on trees of comparable bole size. Genetic influence in crown development has been observed in a number of forest tree species; for example, Ehrenberg (1966) reported a genetic relationship in branch characteristics of Scotch pine, Campbell (1961) has calculated estimates of the variation in branch characteristics to be expected between trees and between populations of Douglas fir; and similar studies of variation in crown characteristics have been made for slash pine (Strickland and Goddard, 1966) and for Cryptomeria (Arita and Tomita, 1964).

Fielding (1953, 1960) studied the genetic influence in crown development of P. radiata and showed clones vary widely in the numbers of whorls produced each year, the size and thickenss of branches, and the density of their crowns. However few quantitative data are available from which the various factors contributing to between-tree variation in crown development, particularly of branch wood and leaf dry weight, can be assessed.

In P. radiata plantations between-tree variation in nutrient content probably partly results from a genetic influence both in physiological capacity of trees to absorb, transport and utilise nutrients, and in their morphology. In a commerical plantation, if trees of similar size have contrasting total nutrient contents then they may differ in ability to absorb nutrients from the soil or have differing efficiencies for the utilization of those nutrients for bole wood production. Trees with greater nutrient content due to a superior absorptive ability might be favoured as parent trees, particularly for planting on low nutrient sites, but where the greater nutrient content results only from greater accumulation then those trees may more quickly exhibit deficiency symptoms and poorer growth on low nutrient

sites, and require greater quantities of fertilizer to achieve maximum growth.

The relative importance of environment and genotype as factors contributing to the substantial variation in total nutrient content of P. radiata trees should be assessed to provide a basis for silvicultural and management decisions regarding thinning, pruning and fertilizer addition, in the interpretation of field experiments of those operations, and so the importance of mineral nutrition in tree improvement selection and progeny testing can be considered.

The present study has been confined to an examination of the relative contribution of genetic and environmental factors to the total variation in nutrient status. Variation in the nutrient content of forest trees has been assessed in a field study using clonal material (Chapter 8.2) and some further observations were made of seedings in a glasshouse with some environmental control (Chapter 9).

8.2 THE STUDY AREA AND METHODS USED

8.2.1 Selection of the study area

Rooted cuttings of selected clones have been extensively planted in A.C.T. plantations for many years by Dr J. Fielding (Forest Research Institute). Numerous parent trees have been selected each year for particular characteristics, including stem form, vigour, wood density, etc., or simply as better than average plantation trees. Cuttings were taken from the current lateral branch growth and established as rooted stock in a nursery (see Fielding, 1954, for details). Some clones have been planted in replicated block experiments but these were not available for destructive sampling; consequently clone blocks were examined where ramets had been established in single lines with contrasting genotypes in adjoining rows.

A block of clones established in 1961 in the Blue Range plantation was selected as the most suitable. The site is at an elevation of approximately 670 m (2200 ft.) above sea level in the foothills of the mountains and about 25 km (15 miles) west of Canberra; the annual rainfall is about 90 cm (35 in) and occasional light falls of snow occur in most winters (Fielding and Brown, 1961). Within the block, six clones were selected which had been planted in single rows (although one clone was in two adjacent rows) at right angles to an access road and at about 2 m x 2 m spacing (Plate 8.1, Fig. 8.1). There was little evidence of site variation across the rows and all six clones showed similar relative development along the row. The lower branches on many of the largest trees were touching branches of adjoining trees, but there was no substantial competition between trees apparent at the time of sampling, six years after planting of the rooted cuttings. Only a small proportion of all leaves grown on each tree had been shed.

The area of the clone block was originally eucalypt forest and after pine planting had been kept clean of woody eucalypt regrowth. A heavy grass cover had become established, particularly in the lower sections away from the road where the original eucalypt cover was evidently less dense. Competition from the grass cover has probably contributed to the variable tree development within each clone.

In a second clone block nearby, rooted cuttings of three of the clones selected for study in the 1961 clone block had also been planted in lines in 1962 (Fig. 8.1, Plate 8.2). Trees in the 1962 area were selected for less intensive examination and provide comparison with the results of the main study. The two study areas were selected and all the trees measured and sampled in July - August, 1967.

8.2.2 Selection of the clone parent trees for propagation

Of the six clones examined, five had been raised from cuttings taken from young plantation seedling trees. The

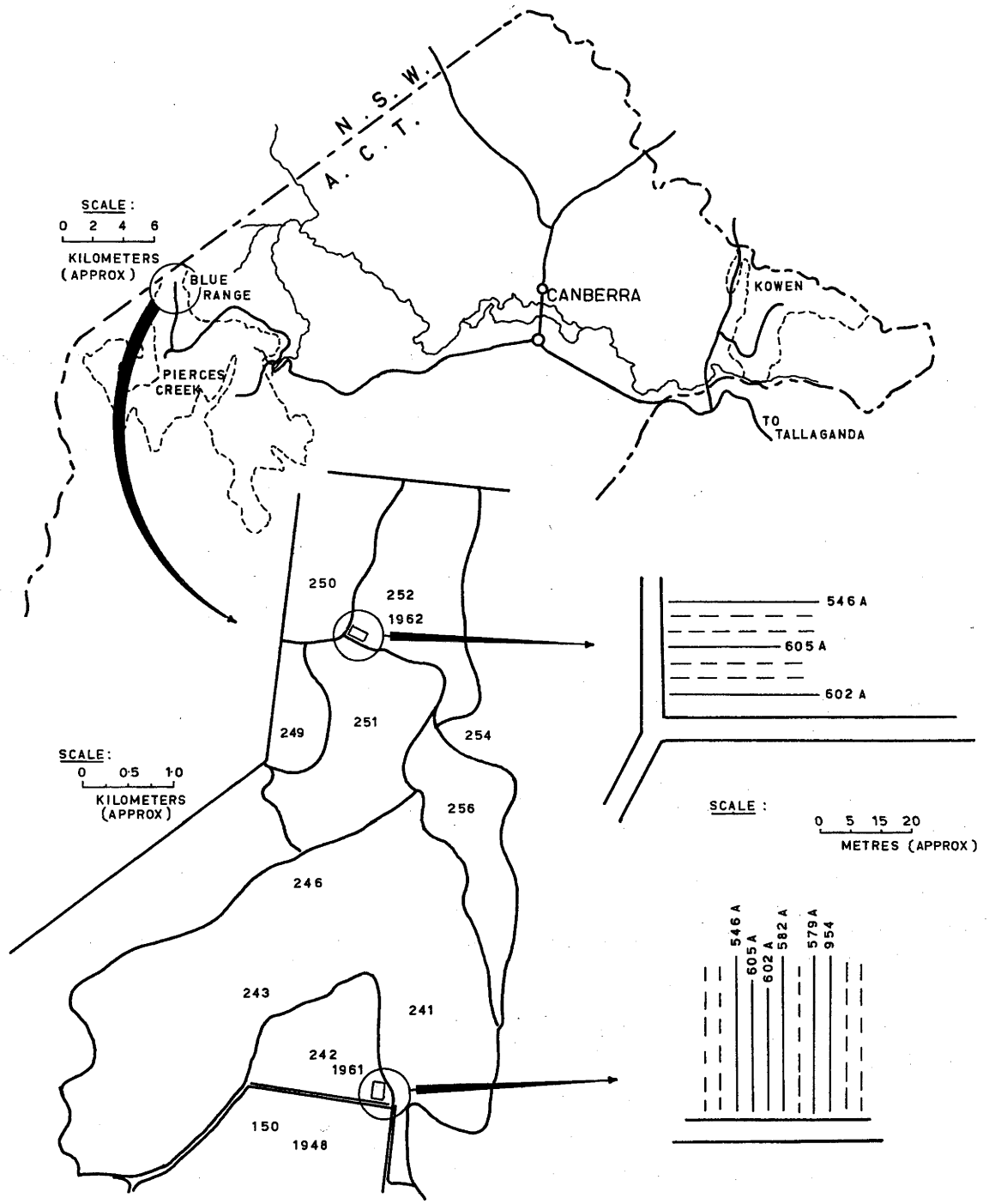


FIGURE 8-1 SKETCH PLAN OF P.RADIATA CLONE BLOCKS

BLUE RANGE PLANTATION

PLATE 8.1 Blue Range plantation. 1961 clone block. Showing first trees in three clone rows, (L to R) clones 546A, 602A and 605A.


605A

PLATE 8.2 Blue Range plantation. 1962 clone block. Showing first trees in two clone rows, clones 546A (left) and 605A (right).


546A
606A

parent trees had all been selected in the routine search for superior phenotypes of above average straightness and vigour, and free from crown damage. The ramets of the sixth clone (954) were a third generation of cuttings propagated from the original parent tree planted in 1934, the second generation trees were 5 years old when cuttings for the 1961 block were taken. The details of parent tree selection, summarised in Table 8.2, were provided by Dr J. Fielding.

8.2.3 Methods of assessment

(a) Mensuration assessment

The first twenty trees in each of the six rows of the 1961 clone block and three rows of the 1962 block were sampled, or all trees were sampled where fewer than twenty trees remained. Some cuttings had failed in most clones but as the study was made before intense competition occurred between trees, the slight variations in spacing along the rows are not critical. The height of all trees and their bole diameters at both 130 cm (4 ft 3 in) and 60 cm (2 ft) were measured.

In the 1961 clone block only, the diameter of each branch on every tree was measured at a point 2.5 cm (1 inch) from the bole, so the branches on each tree could be enumerated by size-classes within whorls. Each branch was measured twice at rightangles using vernier calipers and the average calculated.

(b) Branch weight

After all tree and branch measurements had been made, two branches were cut from each tree in the six clones (rows) of the 1961 block. The branches to be removed were selected randomly from the enumeration of branches for each tree with the prior qualifications that for each clone

(i) all whorls be adequately sampled,

(ii) all branch size classes be equally represented, and (iii) not more than one branch be taken from any one whorl of a tree.

TABLE 8.2 Details of the parent trees of six clones propagated at Blue Range and selected for study

Clone number	Location and description of parent trees			
	Location	Planted	Age when cuttings taken (yrs)	Description
546 A	Cpt 71 Kowen	1955	4	Trunk straight, top good, medium angle branches.
579 A	Cpt 63 Kowen	1954	5	Tall tree in poor area, trunk straight, branches at acute angle.
582 A	Cpt 63 Kowen	1954	5	Branches heavy, medium angle, Trunk straight, good crown.
602 A	Cpt 61 Kowen	1954	5	no details
605 A	Cpt 188 Uriarra	1954	5	Trunk straight, branches evenly spaced, acute angled.
954	Cpt 51 Pierce's Creek	1934*	25*	Very vigorus, branches small, foliage heavy, trunk straight.

* See text, trees in 1961 block are 3rd generation cuttings.

The last proviso was desirable for adequate sampling, but was adopted to limit the effect of branch removal on the subsequent growth of the trees.

Thus forty branches were collected for each clone of twenty trees (with some minor practical variations) but only 34 and 36 branches respectively were taken from the two clones with 17 and 18 sampled trees. All branches were oven-dried at 85°C within 24 hours after collection. When dry, the leaves were removed from each branch and the leaves and wood weighed separately.

(c) Nutrient content of branches

The dried wood and leaves of each branch were finely ground after separation; many branches were small so sampling was not needed, but where the wood or leaves weighed more than about 50 gm these were sampled by quatering before grinding. Small samples of both leaf and wood tissues of each branch were analysed for phosphorus, calcium, potassium, magnesium and zinc concentrations, using the methods described previously (Chapter 5.2).

The weight of each nutrient element in the leaves, wood and total for each branch was calculated from the concentrations and dry weights.

(d) Foliage samples to indicate tree nutrient status.

The nutrient status of a tree is frequently assessed from a single sample of foliage taken from a standardized position within the tree, so a "representative" foliage sample was collected from each tree in both the 1961 and 1962 clone blocks. A sample of 1- year old leaves was taken from mid-way along the most north-facing branch in the lowest whorl initiated during the immediately past year. This position corresponds closely to the standard sampling position adopted by the Forestry Commission of N.S.W. and other organisations.

All leaf samples were dried within 24 hours after collection, finely ground, and analysed for the six nutrients as described previously.

(e) Weight and nutrient content of boles and roots.

Because the clone blocks had been established for other reasons, none could be sampled destructively. Consequently no estimates can be made of variation in bole, root, or total tree nutrient contents. However, past experience suggests nutrient elements are mainly in the crowns of young trees, so an indication of between-tree variation in nutrient content can be assessed from the tree crowns. Using the bole measurements, the nutrient content of the crown of each tree can be expressed in relation to the bole volume.

8.3 RESULTS

8.3.1 Variation in tree mensurational characteristics

(a) Size of trees

The study trees vary in development within each row (clone), the smallest trees have usually less than half the bole diameter and about half the height of the largest tree of the same clone (Table 8.3). The clone averages of height and bole diameter also vary, but this is less than the total variation within clones. The size variation is not consistent with relative position within the clone block, and the relative growth of clones 546A, 602A and 605A is the same in the 1962 block as in the 1961 block.

When all trees of the 1961 block are considered as a single plot the total diameter distribution is similar to the distribution observed in plantations of similar age (e.g. compare Figs. 8.2, 2.4 and 1.1); so the block can be regarded as having normal minor site variation which has resulted in a similar range of sizes for the ramets of each clone, but without a marked or consistent site change across

FIG. 8-2 NUMBERS OF TREES PER SIZE CLASS FOR SIX CLONES AT BLUE RANGE 1961 PLANTATION

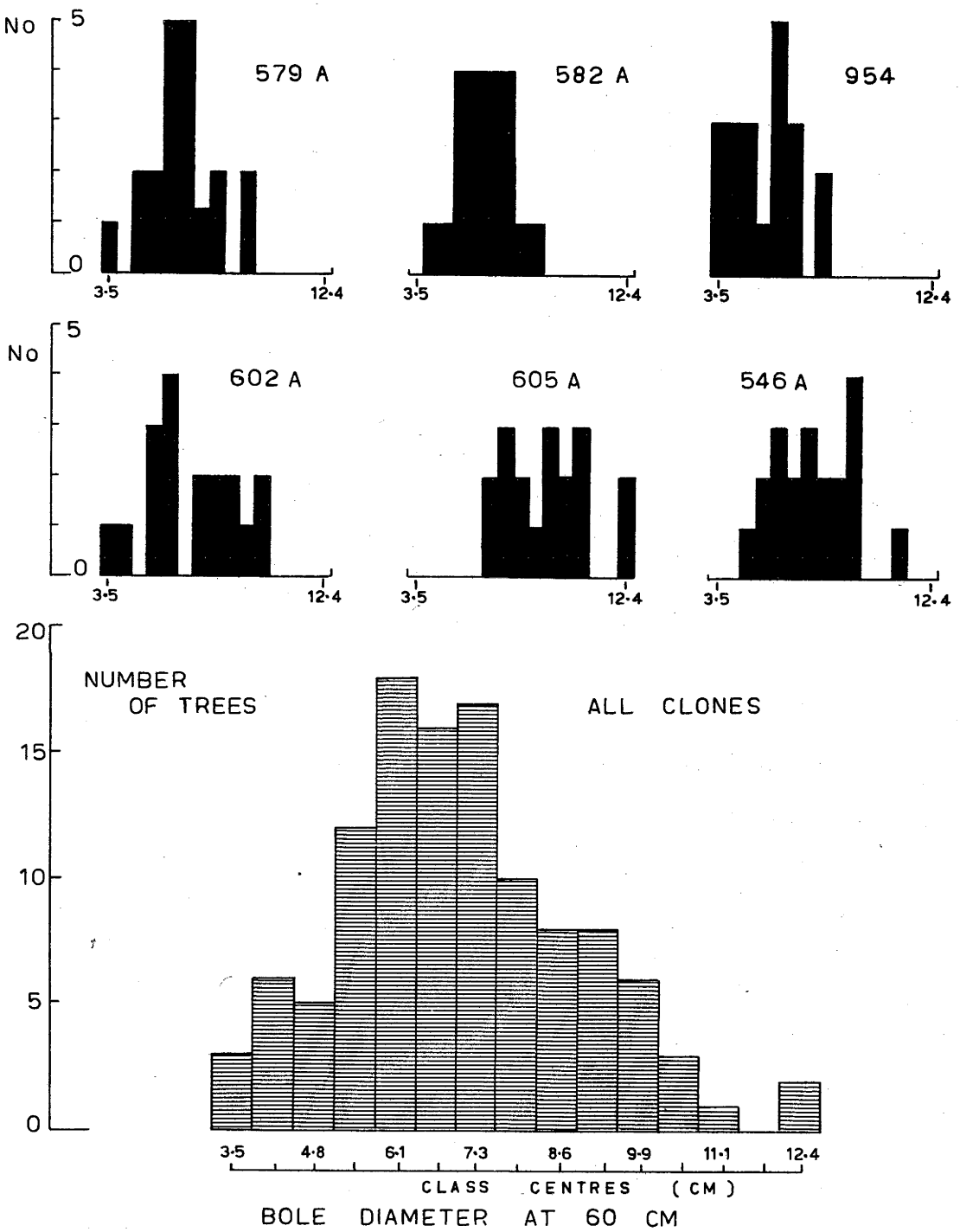


TABLE 8.3 Range of tree sizes in P. radiata clone study

Clone Number	Year Established	Bole Diameter (cm) at 130 cm			Bole Height (m)		
		Min.	Mean	Max.	Min.	Mean	Max.
546 A	1961	3.6	6.6	9.7	3.5	5.2	6.9
579 A	1961	3.4	6.4	9.5	3.2	4.9	5.8
582 A	1961	3.3	5.4	7.5	2.8	4.1	5.4
602 A	1961	3.7	6.0	8.7	3.1	4.4	6.2
605 A	1961	5.4	7.8	10.9	4.1	5.6	6.6
954	1961	2.6	4.6	7.3	2.9	4.0	5.5
546 A	1962	2.7	5.5	9.2	2.6	4.5	6.2
602 A	1962	2.3	5.0	7.7	2.0	3.6	4.9
605 A	1962	3.4	6.2	9.8	3.0	4.7	6.1

the block. Although the clones have been subjectively located and selected, trees of similar size in adjoining rows can be compared for crown weight, weight distribution and nutrient content.

(b) Branch size and the number of branches per tree.

The number of branches per tree and per whorl, and the average branch size per tree can be calculated from the branch enumeration data (Appendices 4-7).

Although all trees in the 1961 block had only been planted 6 years, the numbers of whorls per tree varied considerably, even within clones. For most clones the number of whorls per tree was closely related to tree height, although the relationships varied between clones, for example trees of clone 546A had 8-17 whorls and of clone 602A had 5-11 whorls per tree. In one clone (605A) the number of whorls per tree varied from 9 to 13 but was independent of tree size (Table 8.4). No clone was truly uninodal, although trees of clone 602A had only 1 whorl for most years.

For all clones, the number of branches per tree was closely related to tree bole diameter, but the relationships varied between clones (Fig. 8.3a) and was least significant

for clone 605A for trees of which the number of whorls per tree was least related to tree size (Table 8.4). The average number of branches per whorl varied only slightly between trees of each clone, but the means for all trees varied significantly between clones (Table 8.4). The average branch diameter for each tree was significantly related to tree size, and again the relationships varied between clones (Fig. 8.3b).

Thus there is a consistent genetic influence in the development of tree crowns for the six clones studied. Trees of clone 602A had fewer whorls and branches per tree, but the average branch diameter per tree was greater, and there were more branches per whorl than in other clones. Trees of clones 546A and 579A were mutually similar for most characteristics, with more branches per tree than in most other clones, although 546A had more whorls per tree than other clones. Trees of clone 954 had intermediate numbers of branches and numbers of whorls, but the average branch diameter was less.

8.3.2 Variation in branch weight

Two branches were sampled from each tree and their diameters and dry weights of wood and leaves recorded (Appendix 8). There is a close relationship between branch diameter and either wood or leaf dry weight, so simple linear regressions between branch size and weight are statistically significant, with or without transformation. However direct regressions between diameter and branch weight may be unreliable for the prediction of crown weight, particularly for small trees with smaller than average branches (Fig. 8.4), and so allometric relationships have been calculated for branch wood, leaf and total weights against branch diameter in each clone.

i.e. Log_e Branch weight = a + b Log_e Branch diameter

-- Equation 8.1.

FIG. 8-3 RELATIONSHIPS BETWEEN BOLE SIZE AND BRANCH CHARACTERISTICS FOR TREES IN THE 1961 BLUE RANGE CLONE BLOCK

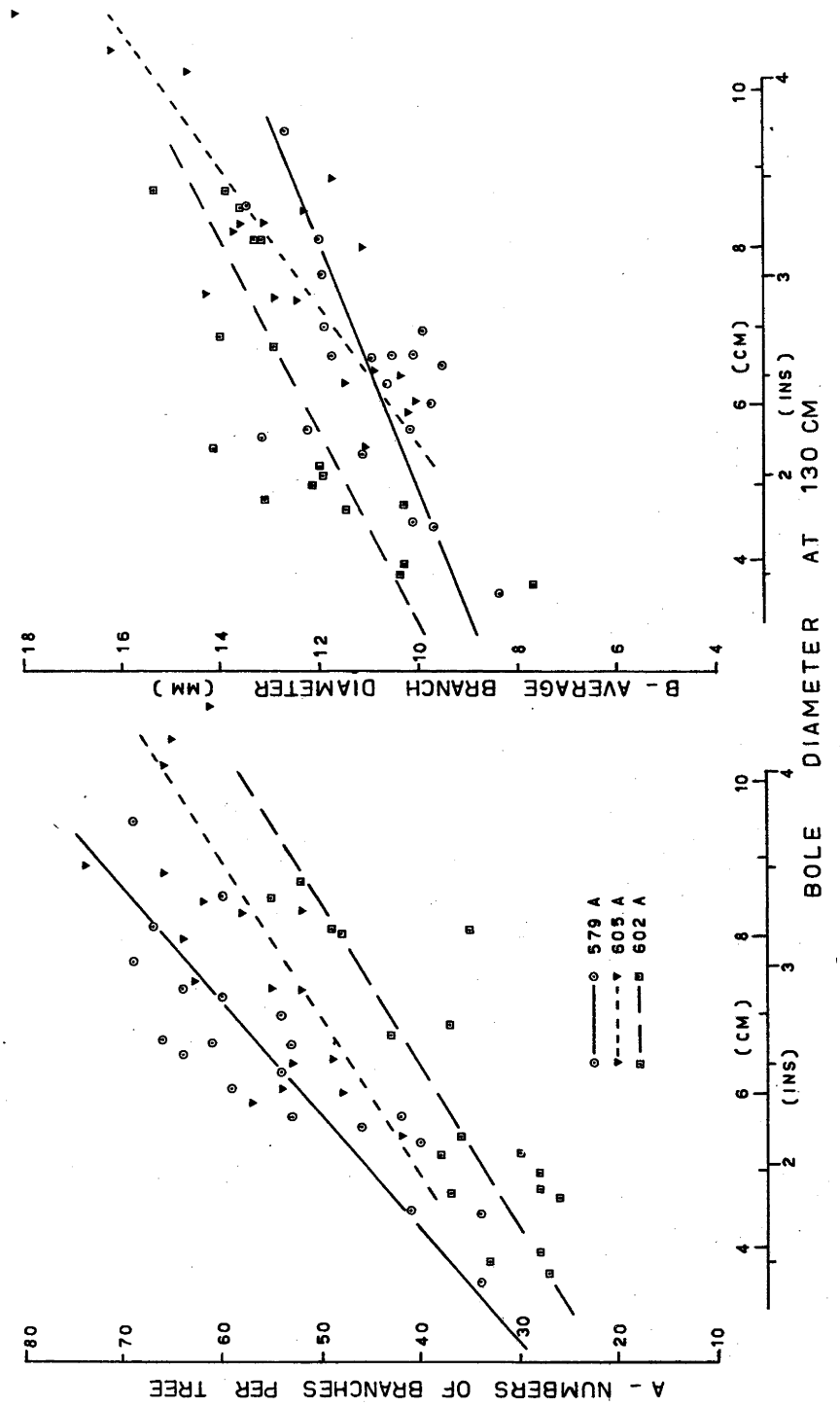
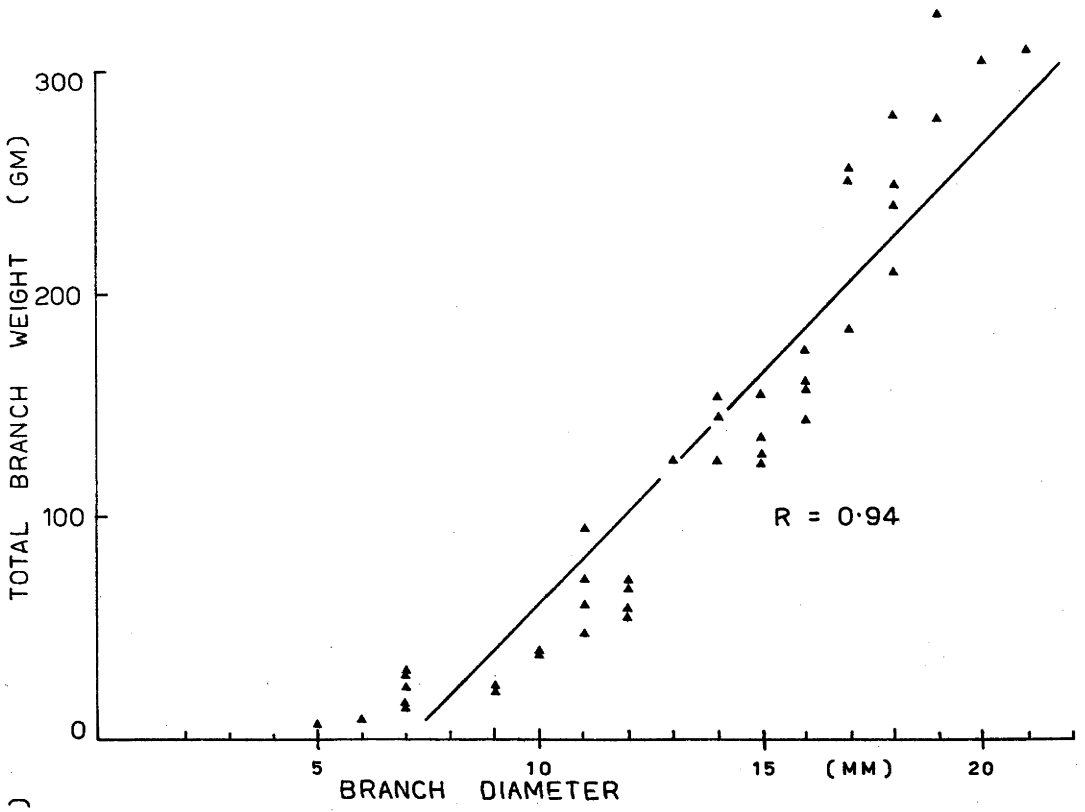


FIG. 8-4 RELATIONSHIPS BETWEEN BRANCH DIAMETERS AND TOTAL BRANCH WEIGHTS FOR TREES OF CLONE 546 A



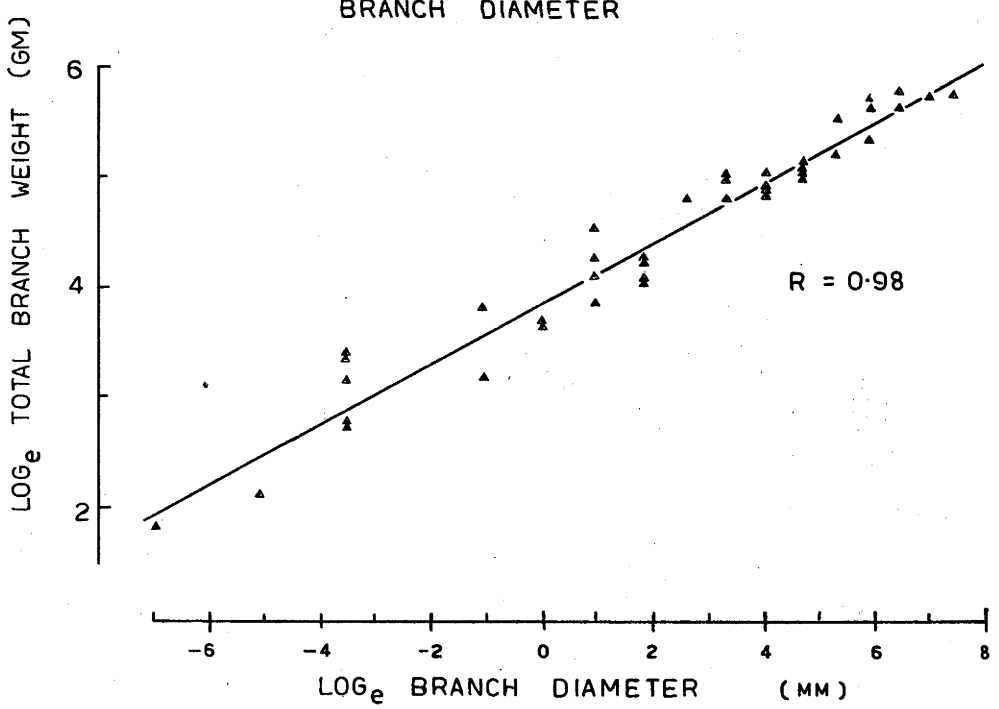


TABLE 8.4 Significance of relationships between crown characteristics and tree size in P. radiata clone study

Values for "b" and "T" (=b/S.E.$_b$) in regressions --- Y = a + b D.B.H.

b is significant at P = 0.0005 when T = 4.42 (n-2 = 15)

b is significant at P = 0.01 when T = 2.95 (n-2 = 15)

b is significant at P = 0.0005 when T = 4.23 (n-2 = 18)

b is significant at P = 0.01 when T = 2.88 (n-2 = 18)

Clone	546A	579A	582A	602A	605A	954
Number of trees (n)	20	20	20	17	18	20
Tree height (m)						
Mean	5.17	4.88	4.15	4.43	5.56	4.00
b	4.82	3.90	4.34	4.74	3.53	5.22
T	16.63	12.18	10.92	17.41	12.04	16.50
Number of branches per tree						
Mean	53.95	54.60	44.15	37.06	57.83	48.65
b	21.42	17.45	14.89	11.10	8.58	20.78
T	10.01	7.37	5.07	5.52	3.96	8.91
Number of whorls per tree						
Mean	12.40	10.30	9.85	7.35	10.83	10.45
b	3.62	2.95	2.92	2.19	0.80	3.13
T	7.32	5.38	4.30	4.70	1.60 (N.S.)	5.80
Average branch diameter per tree (mm)						
Mean	10.62	10.97	10.44	12.32	12.70	7.65
b	1.56	1.60	2.49	2.05	2.88	1.90
T	4.31	4.00	5.02	6.03	7.89	4.82
Average number of branches per whorl						
Mean	4.315	5.309	4.510	5.137	5.352	4.613
Comparison of means arranged in order	546A	582A	954	602A	579A	605A
	4.315	4.510	4.613	5.137	5.309	5.352

Means grouped in brackets are not significantly different at P = 0.05.

Small branches from the top whorls of each tree tended to be lighter than older branches of the same diameter, but since these were a small proportion of all branches and of the sample they have not been considered separately.

All equations relating branch size and weight are highly significant for each clone (P = 0.01, Table 8.5). When corresponding equations for the six clones are compared (using analysis of variance methods described by Williams, 1959), the small variations in slope and position are barely significant (Table 8.6, Fig. 8.5). Thus, the weights of leaves and wood of branches of a given diameter vary only slightly within any clone, but the weight of leaves, particularly, may differ between clones for branches of the same diameter. Branches of clones 582A and 954 differ most in both leaf and wood weight.

The relationships between branch wood weight and leaf weight of the form:

branch weight = a + b branch leaf weight Equation 8.2

have been calculated for all branches in each clone (Table 8.5). The relative increase of the two components with increasing branch size is an important indication of the distribution of total production within the trees. Again, the equation for each clone is highly significant (P = 0.01); and these equations differ markedly between clones (Fig. 8.6). Branches of any particular wood weight differ little within clones but widely between clones in the weight of leaves; for example, the weight of branches of clone 579A is almost equally divided between leaves and wood, but for clone 954 only one quarter of the total branch weight is of wood.

8.3.3 Variation in tree crown weights

The weights of branch wood, leaves and the total weight for the crown of each tree can be estimated by solving in Equation 8.1 for all branches in the tree (Appendix 9). Crown weights have been calculated for all trees in each

TABLE 8.5 *P. radiata* clone study. Regression values and significance of branch size: weight regressions

Log_e branch weight = a + b Log_e branch diameter

and Branch wood weight = a + b Branch leaf weight

Clone	546 A	579 A	582 A	602 A	605 A	954
Degrees of freedom	38	40	37	32	34	38
Branch wood weight x diameter						
a	-4.726	-4.496	-4.078	-4.369	-4.794	-4.953
b	3.201	3.119	2.918	3.072	3.191	3.303
$S.E._b$	0.096	0.126	0.088	0.142	0.125	0.128
R	0.983	0.969	0.983	0.968	0.971	0.972
Branch leaf weight x diameter						
a	-2.244	-2.310	-1.761	-1.880	-2.889	-2.785
b	2.496	2.501	2.258	2.326	2.693	2.826
$S.E._b$	0.111	0.238	0.089	0.160	0.156	0.182
R	0.965	0.860	0.973	0.933	0.937	0.930
Total branch weight x diameter						
a	-2.378	-2.353	-1.842	-2.080	-2.893	-2.711
b	2.713	2.696	2.460	2.582	2.866	2.926
$S.E._b$	0.099	0.183	0.075	0.148	0.129	0.149
R	0.976	0.920	0.983	0.952	0.961	0.954
Wood weight x leaf weight						
a	-8.299	-26.050	-5.720	-8.431	-17.840	-0.504
b	0.691	0.976	0.677	0.762	0.810	0.353
$S.E._b$	0.028	0.049	0.041	0.034	0.034	0.019
R	0.970	0.954	0.938	0.970	0.971	0.949

FIG. 8-5 RELATIONSHIPS BETWEEN BRANCH DIAMETERS AND BRANCH WEIGHTS FOR TREES OF SIX P. RADIATA CLONES

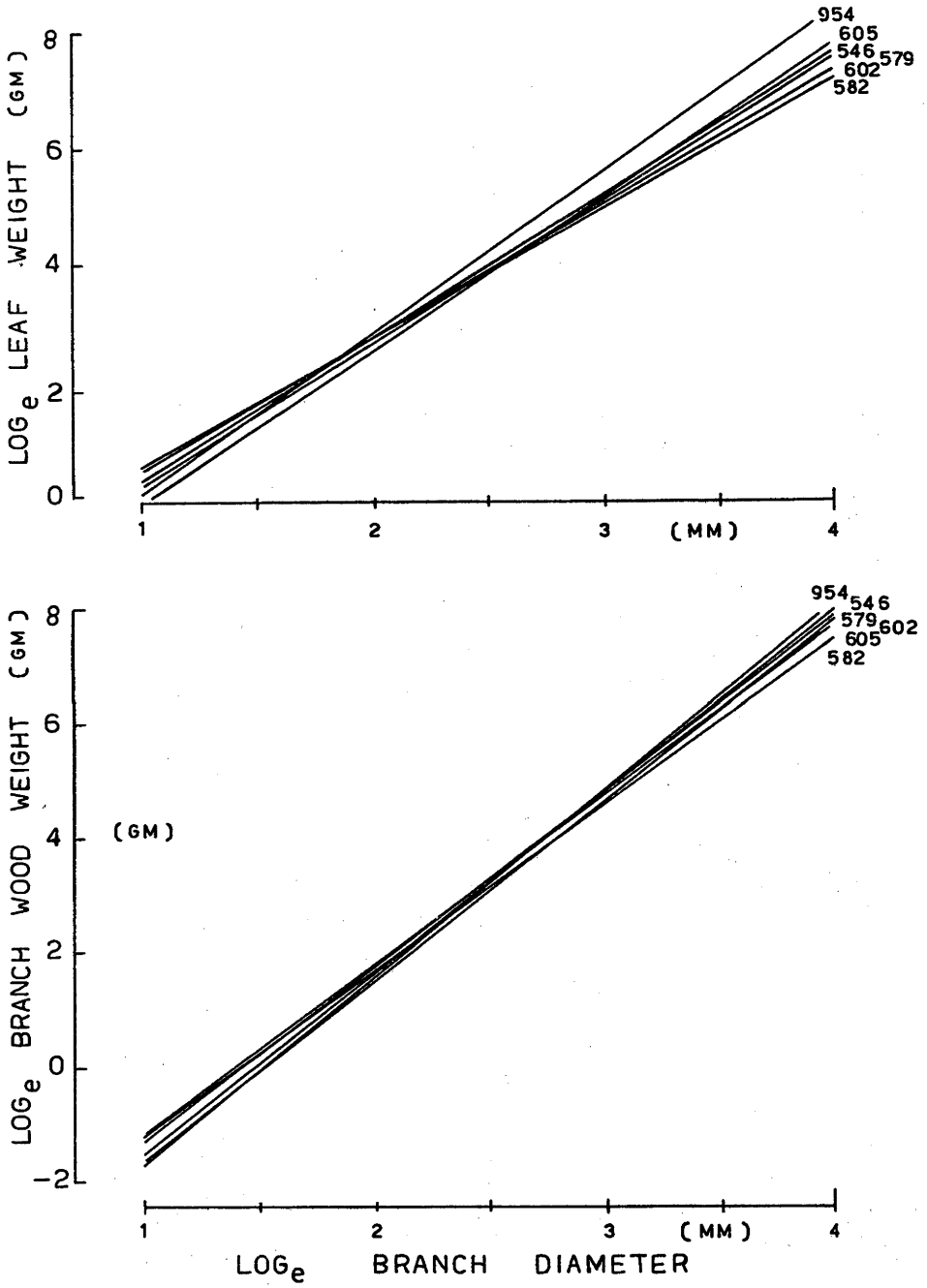


FIG. 8-6 RELATIONSHIPS BETWEEN WEIGHT OF BRANCHES AND CORRESPONDING WEIGHT OF LEAVES FOR TREES OF SIX P.RADIATA CLONES

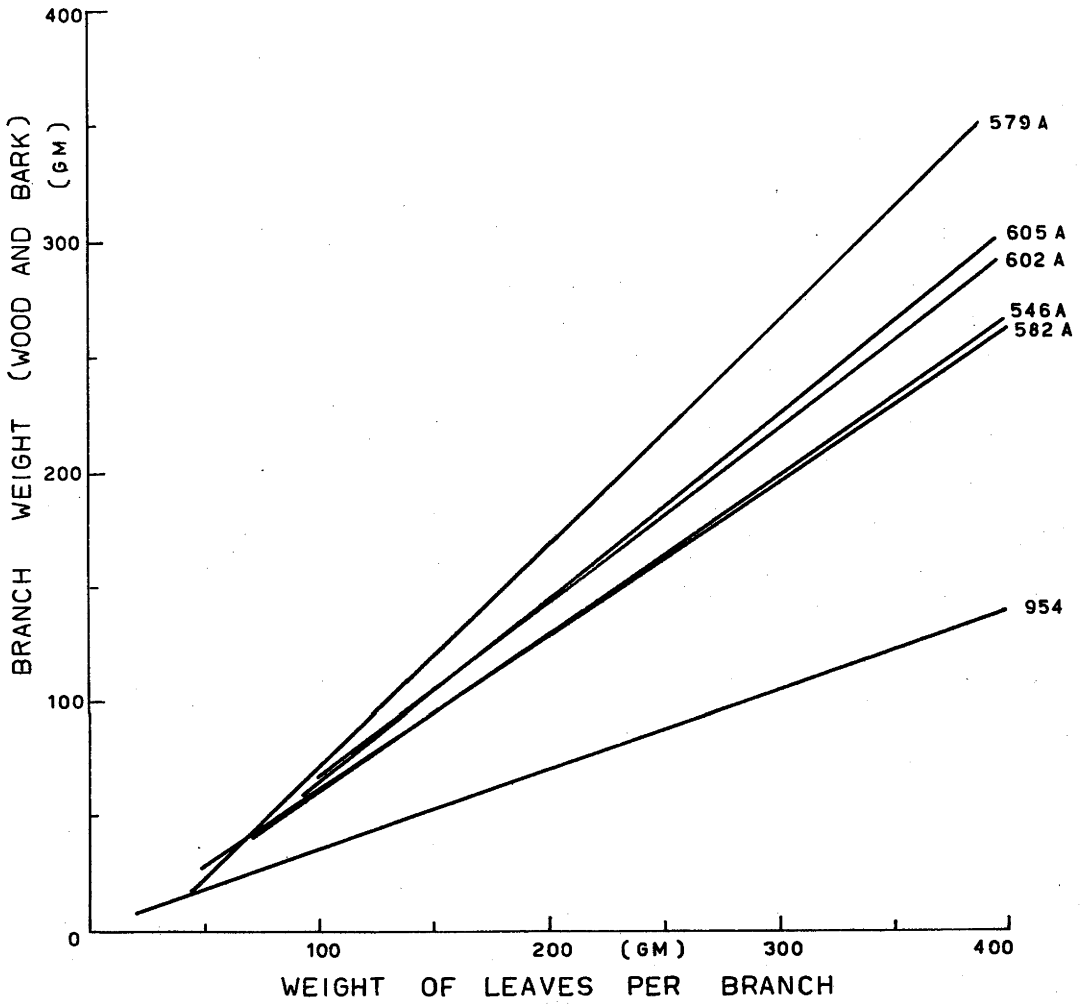


TABLE 8.6 Analysis of variance of regressions of branch weight x size for six P. radiata clones

Source of variation	Degrees of freedom	Mean square	F ratio	Significance
Log_e leaf dry weight = a + b Log_e branch diameter				
Between positions	5	0.0422	0.35	N.S.
Non-parallelism	5	0.2336	1.94	P = 0.10
Log_e branch wood dry weight = a + b Log_e branch diameter				
Between positions	5	0.1114	1.86	P = 0.20
Non-parallelism	5	0.0966	1.61	P = 0.20
Log_e total dry weight = a + b Log_e branch diameter				
Between positions	5	0.0514	0.63	N.S.
Non-parallelism	5	0.1589	1.95	P = 0.10

clone using the regression equation calculated for that clone, even though the equations for each clone may vary only slightly; this is desirable particularly because of differences in branch size distribution between clones.

The relationships between tree size and the estimated branch wood weight, leaf weight and total weight in the tree crowns were then calculated for each clone; equations were of the form:

Log_e crown weight = a + b Log_e bole diameter -Equation 8.3

The equations for each clone are highly significant (P = 0.01, see Table 8.7). The slopes of the equations vary between clones but the differences are not significant; however, the equations differ significantly in position (Table 8.8, Fig. 8.7).

Thus the trees of each clone have characteristic crowns that may be either heavy or light for all tree sizes. The crown weights result from the combined influences of individual branch dry weight and the number of branches per tree, both of which are under genetic control.

FIG. 8-7 RELATIONSHIPS BETWEEN TOTAL CROWN WEIGHT AND BOLE SIZE FOR TREES OF SIX P. RADIATA CLONES

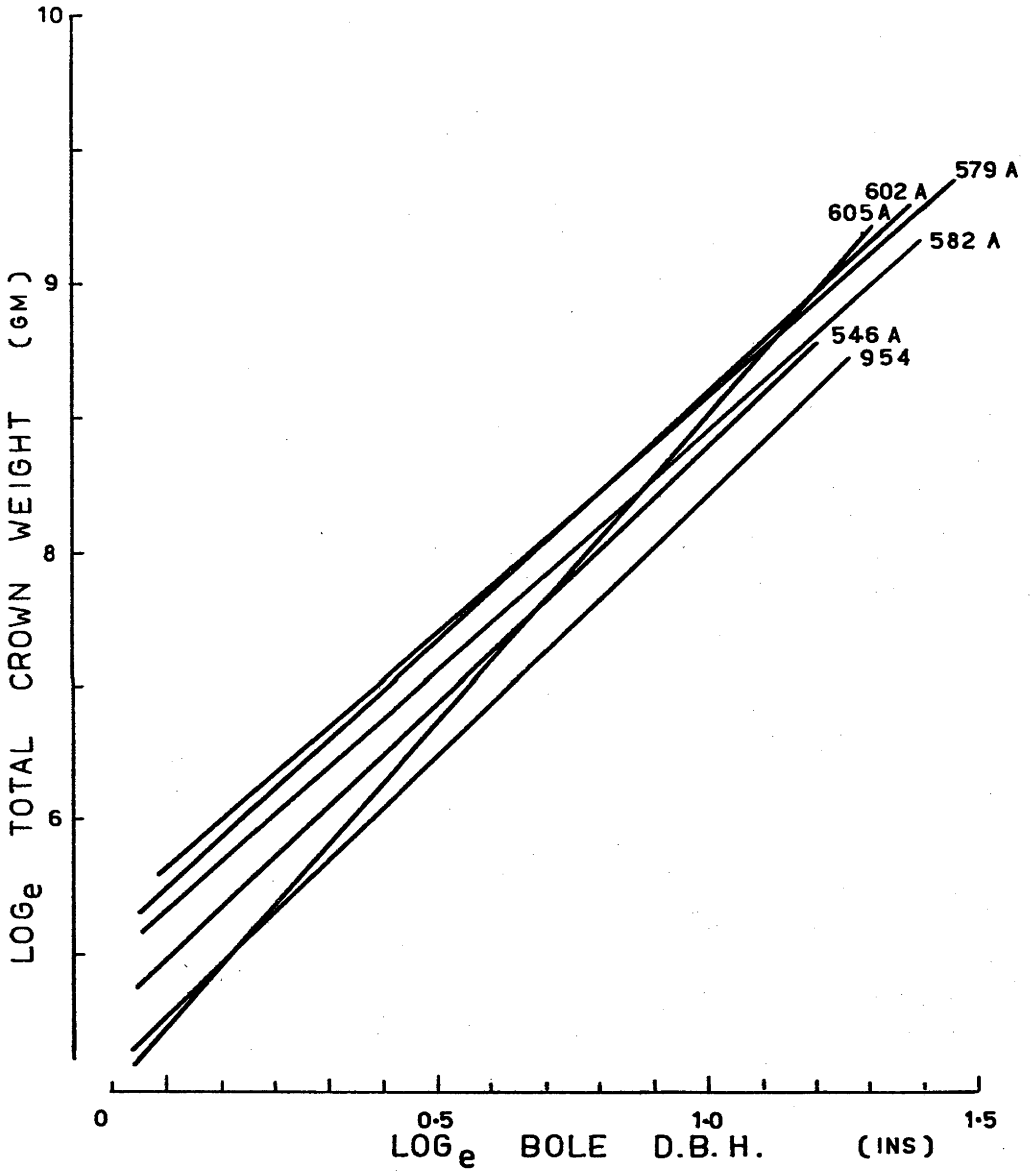


TABLE 8.7 Regression coefficients and the significance of regressions:

Log_e total crown weight = a + b Log_e bole diameter

in P. radiata clone study, Blue Range plantation

Regression value	Clone number					
	546 A	579 A	582 A	602 A	605 A	954
a	6.250	6.595	6.398	6.572	5.951	6.091
b	2.151	1.985	2.058	2.018	2.573	2.185
S.E.$_b$	0.167	0.258	0.194	0.209	0.233	0.061
R^2	0.950	0.876	0.932	0.908	0.941	0.993

TABLE 8.8 Analysis of variance for regression equations:

Log_e total crown weight = a + b Log_e bole diameter

for six P. radiata clones at Blue Range plantation

Source of variation	Degrees of freedom	Mean square	F ratio	Significance
Overall regression	1	33.5956	901.58	
Between positions	5	0.1213	3.26	P = 0.01
Non-parallelism	5	0.0416	1.12	N.S.
Error	103	0.0373		
Total	114			

8.3.4 Variation in nutrient concentrations

Nutrient concentrations have been determined for the leaves and wood from two branches of each tree. When the results for all trees in each clone are combined, the average concentration of nutrients in leaves or wood of each whorl can be assessed, and the overall average concentration of nutrients in leaves, wood and total crown calculated for each clone (Table 8.9). The distribution of nutrients through the crowns of trees varies little within clones, but considerably between clones (e.g. see Fig. 8.8); the

FIG. 8-8 AVERAGE CONCENTRATION OF MINERAL NUTRIENTS THROUGH THE CROWNS OF TREES FOR SIX P.RADIATA CLONES

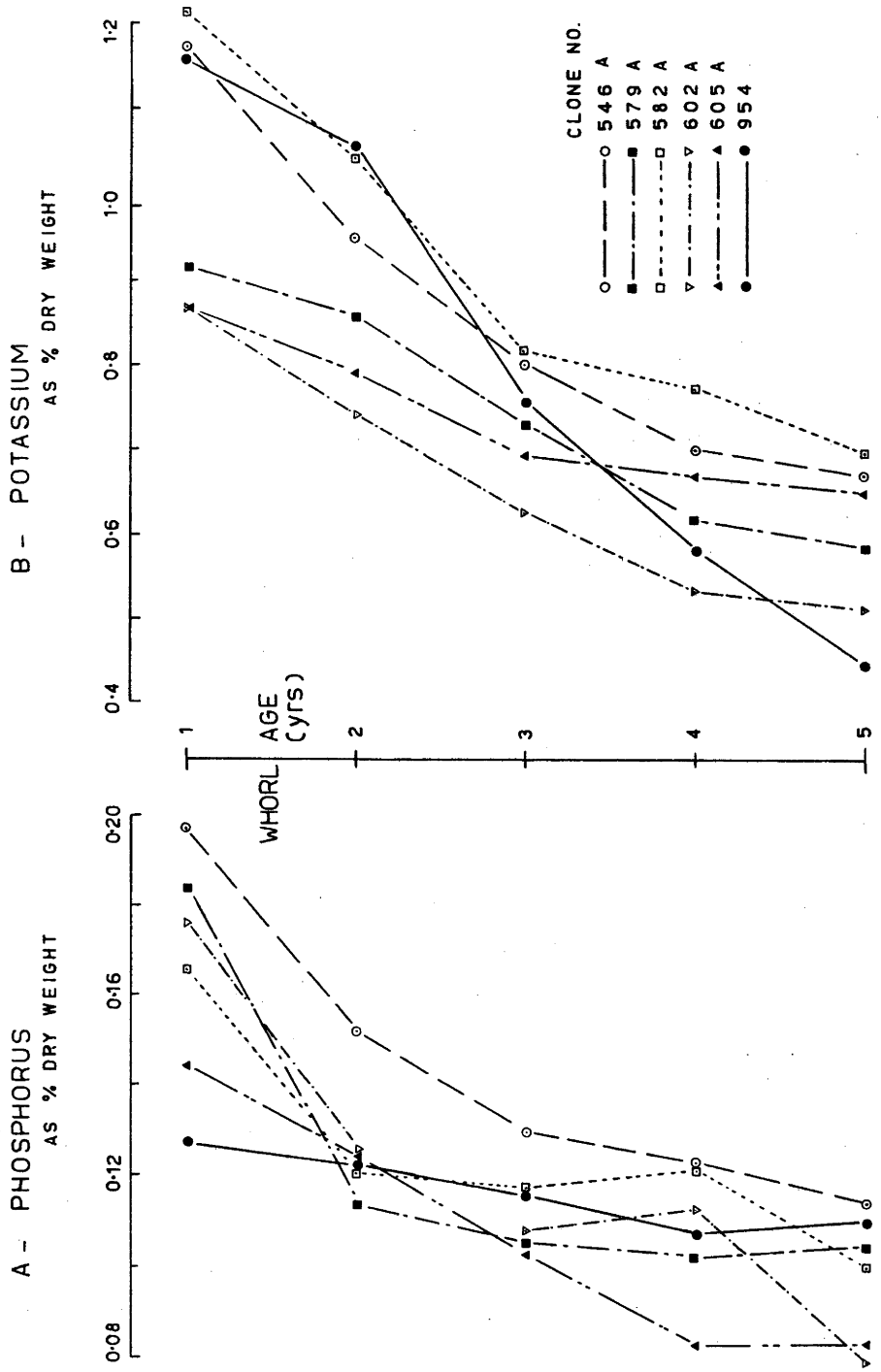


TABLE 8.9 Average nutrient concentration in leaves of all sample branches of the P. radiata clones, Blue Range plantation

Nutrient	Clone number 546 A	579 A	582 A	602 A	605 A	954
Phosphorus % dry weight	0.133	0.110	0.120	0.110	0.099	0.116
Calcium % dry weight	0.475	0.440	0.490	0.460	0.425	0.610
Potassium % dry weight	0.79	0.71	0.81	0.62	0.74	0.75
Magnesium % dry weight	0.160	0.135	0.155	0.150	0.125	0.130
Manganese ppm	285	295	550	340	340	350
Zinc ppm	63	54	82	78	69	45

average concentration of nutrients in the upper whorls, particularly, differ between clones, and 1-year old leaves may inadequately indicate the average nutrient status of the tree. However, overall average concentrations may be unreliable for comparisons within and between clones because of the variation in leaf dry weight and distribution. Variation in nutrient concentrations can be estimated from the concentrations in the standard samples of 1-year old leaves taken from all trees, even though such samples might not represent the tree's average nutrient status.

For each of the six nutrients determined in the standard samples from trees in the 1961 clone block, the concentration means differ significantly between the six clones (Table 8.10). The range of concentrations through the six clones is not the same for all nutrients; for example, the greatest mean phosphorus concentration is 40% greater than the least, but for zinc the greatest is 88% greater than the least. Also, the clones do not consistently contain either a high or low concentration of all nutrients, for example the foliage samples of clone 954 have a high concentration of phosphorus,

magnesium and manganese, but a low concentration of calcium, potassium and zinc, whilst this pattern is reversed for clone 579 A (Table 8.11).

TABLE 8.10 Analysis of variance of mean nutrient concentration in standard samples of one-year old leaves from six P. radiata clones, Blue Range plantation

Source of variation	Degrees of freedom	Mean square	F ratio	Significance ** = Significant at P = 0.01
Phosphorus				
Clones	5	0.00683	11.91	**
Residual	109	0.00057		
Calcium				
Clones	5	0.01685	7.38	**
Residual	109	0.00228		
Potassium				
Clones	5	0.46966	41.84	**
Residual	109	0.01122		
Magnesium				
Clones	5	0.01301	37.35	**
Residual	109	0.00035		
Manganese				
Clones	5	46582.4	4.78	**
Residual	109	9751.2		
Zinc				
Clones	5	2021.3	23.31	**
Residual	109	86.7		

TABLE 8.11 Summary of means and significant differences between clones for nutrient concentrations in standard samples of 1- year old foliage from trees in 1961 clone block, Blue Range plantation
Comparison of means by Tukey's T- test

Phosphorus (% dry weight)		Calcium (% dry weight)	
579 A	0.126	546 A	0.179
605 A	0.139	954	0.199
602 A	0.150	605 A	0.203
582 A	0.165	579 A	0.233
546 A	0.167	602 A	0.235
954	0.175	582 A	0.258
Potassium (% dry weight)		**Magnesium (% dry weight)**	
602 A	0.772	546 A	0.091
954	0.784	605 A	0.094
579 A	0.924	579 A	0.121
546 A	1.018	602 A	0.139
605 A	1.037	582 A	0.141
582 A	1.176	954	0.153
Manganese (ppm)		**Zinc (ppm)**	
546 A	164	954	35
579 A	194	605 A	47
605 A	218	546 A	48
954	255	579 A	49
602 A	258	582 A	57
582 A	298	602 A	66

Means grouped within a bracket are not significantly different at P = 0.05.

TABLE 8.12 Comparison of variation in nutrient concentrations for standard samples of 1- year old foliage from trees of three clones in 1961 and 1962 clone blocks, Blue Range plantation. Comparison of means by Tukey's T- test. Means grouped within a bracket are not significantly different at P = 0.05

Nutrient	Clone block	Clone and nutrient mean concentration		
Phosphorus (% dry weight)	1961	605 A 0.139	602 A 0.150	546 A 0.167
	1962	602 A 0.148	605 A 0.151	546 A 0.187
Calcium (% dry weight)	1961	546 A 0.179	605 A 0.203	602 A 0.235
	1962	546 A 0.186	605 A 0.209	602 A 0.214
Potassium (% dry weight)	1961	602 A 0.772	546 A 1.018	605 A 1.037
	1962	602 A 0.795	605 A 1.058	546 A 1.125
Magnesium (% dry weight)	1961	546 A 0.091	605 A 0.094	602 A 0.139
	1962	605 A 0.096	546 A 0.104	602 A 0.139
Manganese (ppm)	1961	546 A 164	605 A 218	602 A 258
	1962	605 A 160	602 A 160	546 A 166
Zinc (ppm)	1961	605 A 47	546 A 48	602 A 66
	1962	546 A 38	605 A 42	602 A 45

Similar standard foliage samples were analysed for the trees in the 1962 clone block and similar results obtained; the three clones differ significantly in the concentrations of nutrients (Table 8.12). In addition, the differences between clones in the 1962 block are remarkably similar to differences in the 1961 block (Table 8.12), even though there are small differences in the concentrations of nutrients for each clone at the two localities. At the probability level, P = 0.05, the results for the two clone blocks are identical for phosphorus, potassium and magnesium, and nearly so for calcium, manganese and zinc; for example the calcium concentration in the foliage from trees of clone 546 A is significantly less than that of 602 A in the 1961 block at P = 0.05, and in the 1962 block at P = 0.10. There are no major differences in soil type evident between the two clone blocks, so generally similar results might be expected; however the sites differ in aspect, position on slope and degree of slope and are about 2 km apart, so it is most unlikely that site variation within both blocks be identical with respect to the positions of the three clones in each block. Thus, it may be concluded that the variation in nutrient concentrations between clones of the 1961 block is due mainly to genetic influences.

8.3.5 Variation in nutrient content of sample branches

The weights of nutrients in the leaves and wood of each of the sample branches were calculated from the nutrient concentration and dry weight values. The relationships between branch diameter and nutrient weights in leaves, wood or total branch were then calculated, the regression equations being of the same form as for dry weight (Equation 8.1). All regression equations were highly significant (Table 8.13), even though the average concentration of nutrients varied for branches of similar diameter within each clone, depending on the height of the branch in the tree crown.

TABLE 8.13 Regression constants and significance of regressions calculated to define total weight of nutrients in branches of P. radiata trees in clone study, Blue Range Plantation.
Equations of form:
Log_e nutrient weight = a + b Log_e branch diameter
For significance (P = 0.001, n = 35), T(=b/S.E.$_b$) = 3.6

Nutrient	Clone number					
	546 A	579 A	582 A	602 A	605 A	954
n	40	42	39	34	36	40
Phosphorus						
a	-7.703	-8.292	-7.810	-8.343	-8.626	-9.199
b	2.152	2.327	2.079	2.309	2.382	2.753
T	30.6	21.6	23.0	26.7	21.4	17.2
Calcium						
a	-10.904	-8.397	-8.685	-7.914	-10.551	-8.684
b	3.746	2.820	2.939	2.576	3.503	3.197
T	12.7	9.2	16.4	6.8	11.8	10.3
Potassium						
a	-6.023	-6.723	-5.636	-6.845	-6.458	-7.429
b	2.223	2.468	2.006	2.442	2.343	2.827
T	29.3	13.3	22.1	26.5	19.2	21.6
Magnesium						
a	-9.820	-8.590	-8.636	-8.403	-10.135	-9.116
b	3.002	2.539	2.535	2.450	2.994	2.787
T	16.1	16.9	24.8	12.1	16.7	18.7
Manganese						
a	-2.441	-1.597	-1.686	-0.801	-2.697	-1.076
b	2.981	2.679	2.909	2.415	3.104	2.613
T	10.2	7.3	11.8	7.8	10.9	6.7
Zinc						
a	-3.477	-3.062	-2.903	-2.097	-4.074	-3.665
b	2.901	2.714	2.727	2.412	3.063	2.952
T	16.0	11.2	17.9	9.6	13.0	11.7

The regression equations calculated for the weights of phosphorus, calcium, potassium and magnesium in branches differ widely between the several clones (Table 8.14). The equations for weight of manganese differ slightly in position, and of zinc differ slightly in slope ($P = 0.25$). These differences result from the small differences in dry weight between clones (Table 8.6) together with the irregular differences in average nutrient concentrations (Tables 8.9; 8.11). Where clones differ in either dry weight or nutrient concentration the differences in branch nutrient content may be large. But differences between clones in both branch dry weight and nutrient concentration may be complimentary, and result in similar weights of nutrients in branches of similar diameter. Lack of significant difference between regressions may also occur when the within-clone variation in nutrient concentration is great (e.g. for manganese).

Thus, branches from trees in the 1961 clone block differ little in nutrient content (for a given branch diameter) within each clone, but differ substantially between clones. The variation between clones for each nutrient depends on variation between clones in branch dry weight, in nutrient concentration, and the interaction of these, and the variance within each clone, particularly in nutrient concentration.

8.3.6 Variation in nutrient content of tree crowns

The amounts of nutrients in the crown of each tree has been estimated by solving the appropriate branch nutrient weight x branch diameter regression equations for all branches in the tree (as for crown dry weight). The regression equation for the particular clone was used rather than a combined equation, even where regressions did not differ significantly, because of the variable branch size distribution between clones. Regression equations were then calculated, using the form of Equation 3 for crown dry weight, to define the relationships between bole size and the

TABLE 8.14 Analysis of variance summary for regression equations : Log_e nutrient weight = a + b Log_e branch diameter for six P. radiata clones, Blue Range plantation

Source of variation	F ratios and level of significance					
	Nutrients in leaves		Nutrients in wood		Total nutrients in branches	
Phosphorus						
Between positions	0.13	(N.S.)	1.39	(0.25)	0.18	(N.S.)
Non-parallelism	3.82	(0.01)	2.68	(0.05)	4.56	(0.01)
Calcium						
Between positions	0.86	(N.S.)	1.39	(0.25)	0.97	(N.S.)
Non-parallelism	2.75	(0.05)	1.96	(0.25)	2.74	(0.05)
Potassium						
Between positions	0.75	(N.S.)	1.55	(N.S.)	0.84	(N.S.)
Non-parallelism	3.66	(0.01)	5.08	(0.01)	5.10	(0.01)
Magnesium						
Between positions	0.71	(N.S.)	2.06	(0.10)	1.04	(N.S.)
Non-parallelism	2.59	(0.05)	2.43	(0.05)	2.82	(0.05)
Manganese						
Between positions	1.36	(0.25)	2.16	(0.10)	1.54	(0.25)
Non-parallelism	0.93	(N.S.)	1.04	(N.S.)	1.00	(N.S.)
Zinc						
Between positions	0.65	(N.S.)	1.26	(N.S.)	0.88	(N.S.)
Non-parallelism	1.23	(N.S.)	1.38	(0.25)	1.36	(0.25)

(Figures in brackets indicate the probability level at which the regression equations for the six clones differ significantly).

estimated weight of nutrients in the crown for the trees of each clone (Table 8.15). The equations for all nutrients and clones were highly significant (P = 0.01), so equations for each nutrient were examined for variation in slope and position between clones by analysis of variance (Table 8.16).

TABLE 8.15 Regression coefficients and significance of regressions : Log_e nutrients in crown = a + b Log_e bole diameter for six P. radiata clones at Blue Range plantation.
For significance (P = 0.01, n = 18), T (=b/S.E.$_b$) = 2.90

Nutrient and regression values	Clone number (and n)					
	546 A 20	579 A 20	582 A 20	602 A 17	605 A 18	954 20
Phosphorus						
a	-0.272	-0.169	-0.372	-0.316	-0.749	-0.783
b	1.892	1.817	1.832	1.870	2.218	2.094
T	14.6	8.9	11.7	9.8	12.1	36.1
Calcium						
a	-0.015	0.834	0.586	0.726	-0.383	0.568
b	2.640	2.040	2.337	2.014	3.027	2.328
T	10.8	7.3	9.4	9.6	9.8	33.7
Potassium						
a	1.554	1.712	1.649	1.487	1.339	1.127
b	1.926	1.883	1.789	1.940	2.191	2.130
T	14.2	8.4	11.9	9.8	12.2	35.5
Magnesium						
a	-0.568	0.001	-0.235	-0.052	-1.027	-0.635
b	2.289	1.917	2.100	1.945	2.666	2.109
T	12.2	8.2	10.4	9.8	10.8	36.4
Manganese						
a	-2.434	-1.886	-1.726	-1.739	-2.572	-2.146
b	2.268	1.964	2.239	1.927	2.743	2.040
T	12.1	7.7	4.5	9.8	10.6	40.0
Zinc						
a	-3.647	-3.286	-3.292	-3.048	-4.036	-4.075
b	2.234	1.998	2.204	1.929	2.714	2.182
T	12.4	7.7	9.8	9.7	10.6	34.6

TABLE 8.16 Analysis of variance summary for regression equations : Log_e (weight of nutrients = a + b Log_e bole diameter in tree crown)

Source of variation	Degrees of freedom	Mean square	F ratio	Significance (Equations differ at level shown)
Phosphorus				
Between positions	5	0.09265	3.68	0.01
Non-parallelism	5	0.02453	0.97	N.S.
Error	103	0.02519		
Calcium				
Between positions	5	0.15138	2.82	0.05
Non-parallelism	5	0.12817	2.39	0.05
Error	103	0.05359		
Potassium				
Between positions	5	0.10216	3.78	0.01
Non-parallelism	5	0.02465	0.91	N.S.
Error	103	0.02705		
Magnesium				
Between positions	5	0.10986	2.94	0.05
Non-parallelism	5	0.06628	1.77	0.25
Error	103	0.03742		
Manganese				
Between positions	5	0.16629	2.43	0.05
Non-parallelism	5	0.08896	1.30	N.S.
Error	103	0.06844		
Zinc				
Between positions	5	0.12936	3.20	0.01
Non-parallelism	5	0.06009	1.49	0.25
Error	103	0.04041		

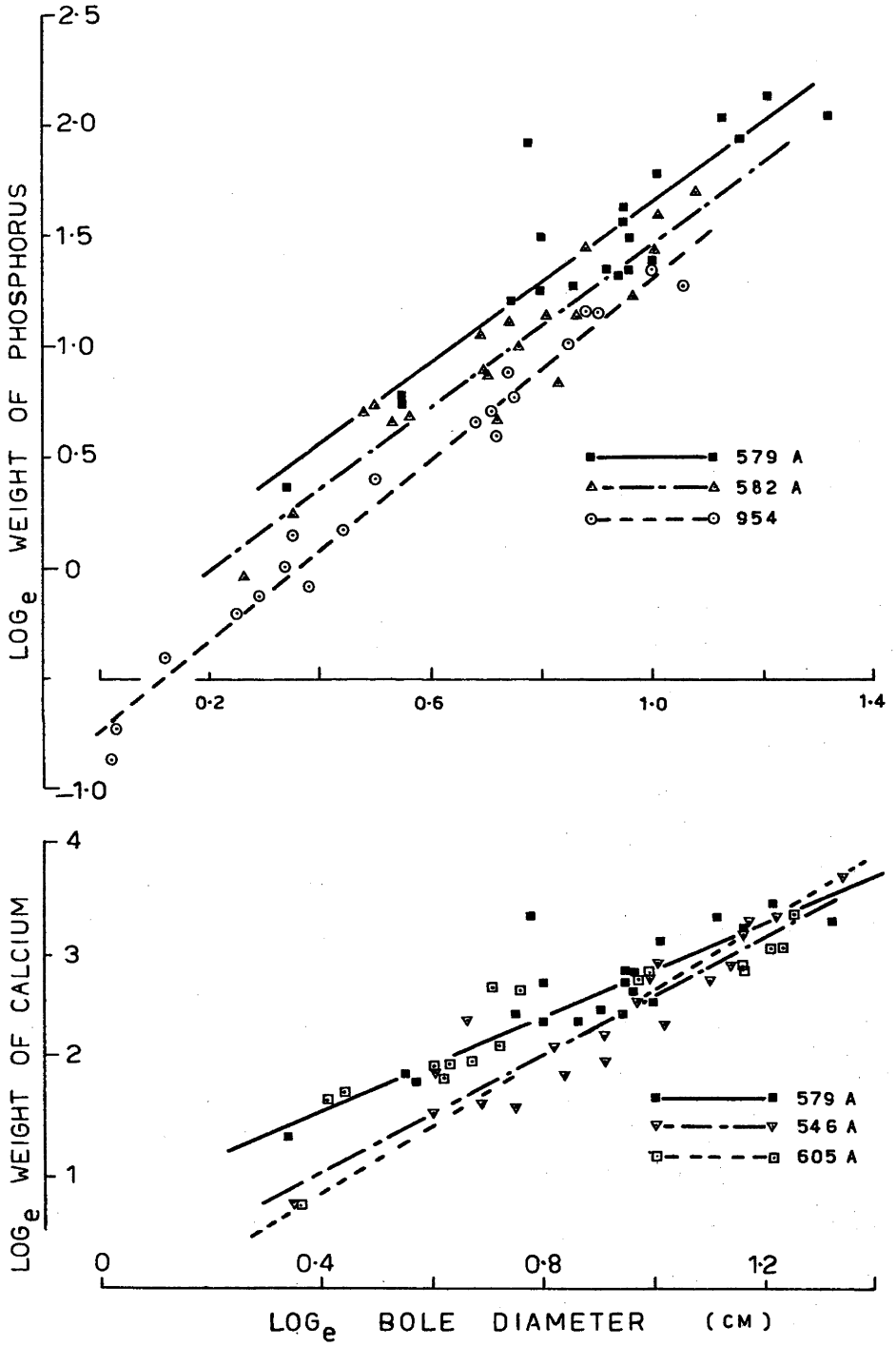
Only for calcium does the slope of the regression vary significantly between clones ($P = 0.05$), but for all nutrients examined the regressions differ in position (Table 8.16, Fig. 8.9). The nutrient content of the crown of any tree depends on the number of branches, the average weight of branches and the average concentration of nutrients contained; any or all of these may vary between clones, and the interactions between the variation in all three will determine the degree of variation between clones in the total nutrient content of the crowns.

8.4 DISCUSSION

The six clones studied were propagated by cuttings from trees in commercial plantations of the A.C.T. The parents were all selected because of phentotypic superiority in characteristics considered desirable in plantation trees, i.e. straight bole, good vigour and healthy crown. The average selection rate was commonly about 2 trees per hectare, or 2%, so trees in the clone blocks are overall less variable than the plantation trees. The six clones examined probably represent only a small band of the overall variation between trees for most characteristics. Nevertheless, there is considerable variation between the six clones for nearly every characteristic measured.

The small differences in average development between clones might be due to variation in reaction to the site, or to differences in vigour. However, the differences in average growth do not account for the variations in other characters assessed; for example, trees of clone 605A and 954 have, on the average, the greatest and least diameters and heights, respectively, yet regressions of branch weight x branch diameter are not significantly different for these clones but both differ significantly from that for clone 582A, and both clones have greater calcium and lesser manganese concentrations in the foliage than clone 546A.

FIG. 8-9 RELATIONSHIPS BETWEEN TOTAL WEIGHT OF NUTRIENTS IN THE CROWN AND BOLE DIAMETER FOR TREES OF SEVERAL P. RADIATA CLONES



Between-clone variation in dry weight and nutrient content cannot reasonably be attributed to within-site variation because site variation along the rows, which are up to 50 m long, is far greater than between rows only 2 m apart, the pattern of variation between clones is inconsistent with the position of clones within the block for all characteristics measured, and the relative development of trees and their foliar nutrient concentrations in the 1961 block are virtually identical with the results from the 1962 block for the three clones located in both blocks. Thus, despite experimental limitations, the results can be regarded as indicative of the variation present in plantations. Differences peculiar to trees of clone 954 may be due in part to their greater physiological age. In 1967 young tissues of most clones were 14 years from seed, but in clone 954 were 34 years from seed. Some evidence for differences in growth of vegetatively propagated material of contrasting physiological age has been reported (Sweet, 1964), but any effects of differing physiological age cannot be assessed in this study. However, clone 954 varied from other clones mostly in branch size and dry weight characteristics which were observed on the parent tree at the time of first selection; in fact the small, light branches on the parent tree have made climbing for seed collection notoriously difficult. The assessed differences are probably largely due to genetic diversity between the parent trees.

Variations between clones in the distribution of organic matter production is illustrated by the differences in relative amounts of branch wood and leaves on branches. The clones also differ in the volume[1] of bole wood produced per unit

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[1] Bole volume was calculated for each tree by assuming the bole to be cylindrical below 2 ft (61 cm) and conical above.

i.e. Bole volume $= \frac{\pi D^2}{3x4}(H-2) + \frac{\pi D^2}{4} \times 2$ D = diameter (D.B.H) H = tree height

weight of leaves (Table 8.17); for example, clone 605A has 30% fewer leaves per unit of bole volume than clone 579A.

TABLE 8.17 Foliage and branch wood weight per unit bole volume for six P. radiata clones at Blue Range plantation (kg per cu m)

Foliage		Branch wood	
Mean dry weight	Clone	Mean dry weight	Clone
262.	605 A	96.	954
279.	546 A	147.	546 A
282.	602 A	169.	582 A
284.	954	211.	605 A
312.	582 A	228.	579 A
367.	579 A	263	602 A

Note : Means grouped within a bracket are not significantly different at P = 0.05

The trees probably differ in bole density, bark thickness and stem form, so the estimates of bole volume might not be consistently related to bole dry weight, however the overall effect of these factors is unlikely to account for the large differences in bole wood production. Differences in production per unit leaf weight could result from many factors, for example, differences in average leaf life, in duration of photosynthesis during each year, in total respiration, in distribution of production between components, or in actual efficiency of photosynthesis and other metabolic processes. Whatever the cause, such differences in foliage efficiency for bole wood production would be an important factor in the achievment of optimum production of useable material in plantations. The differences in crown weight distribution certainly influence considerably the accumulation and distribution of nutrient elements.

Differences between clones in nutrient concentrations have been estimated for the leaves of the whole canopy (Table 8.9) and for 1-year old leaves (Table 8.11). The

nutrient concentrations assessed for a small sample of leaves do not consistently reflect the average nutrient status of the trees because of differences between clones in the changes in average concentration with depth through the crown; for example, the average concentration of potassium in leaves decreases with depth from the apex, but the decrease is dissimilar for all clones (Fig. 8.8). Differences in the rate of change in average concentration probably arise in part because of differences in the proportion of old and young leaves, but probably also because of differences in the amounts of nutrients retranslocated from or deposited in older leaves.

The determination of average nutrient content might be important in some studies, and misleading conclusions may be drawn from estimates of nutrient concentration in small samples; for example, Steinbeck (1966) examined the concentration of nutrients in "one upper lateral branch" of trees in a Scotch pine progeny test and concluded that differences in the nutrient concentrations of such samples demonstrated differences between provenances in ability to accumulate nutrients. Clones 954 and 605A differ markedly in potassium concentration of young leaves but have nearly identical average concentration for the whole crown, and do not differ in amounts of bole wood produced per unit of potassium in the crown (Table 8.18).

These differences in concentrations between clones do not invalidate the use of foliar sampling for diagnostic purposes in plantations or experiments where the genetic composition is mixed, however variation from this source should be considered to ensure adequate sampling.

The nutrients contained in the crowns of small trees are commonly 70-80% of the total nutrients above ground (Chapter 5.3.4) and the concentrations of nutrients in the leaves is closely related to the concentrations in the

TABLE 8.18 Mean weights in total crown per unit bole volume (kg per cu m) of organic matter and nutrients for six *P. radiata* clones at Blue Range

Total dry weight						
Clones:	954	546A	605A	582A	602A	579A
Mean weight :	380.	426.	474.	481.	545.	595.
Phosphorus						
Clones :	605A	954	582A	602A	546A	579A
Mean weight :	0.39	0.40	0.47	0.49	0.49	0.58
Calcium						
Clones :	546A	605A	602A	954	582A	579A
Mean weight :	1.29	1.42	1.57	1.75	1.78	1.98
Potassium						
Clones :	954	605A	602A	546A	582A	579A
Mean weight :	2.74	3.08	3.16	3.17	3.42	4.07
Magnesium						
Clones :	954	605A	546A	582A	602A	579A
Mean weight :	0.46	0.49	0.53	0.65	0.68	0.76
Manganese						
Clones :	546A	954	605A	579A	602A	582A
Mean weight :	0.08	0.10	0.11	0.12	0.13	0.18
Zinc						
Clones :	954	546A	605A	579A	582A	602A
Mean weight :	0.016	0.023	0.026	0.031	0.033	0.034

Note: Means grouped within a bracket are not significantly different at P = 0.05

bole, so the differences assessed between clones in crown nutrient content reflect closely the overall effects of genetic composition on the nutrient content of trees at this age. They also indicate differences in the rate of accumulation during the period of rapid crown expansion when the rate of nutrient requirement from the soil is greatest (Chapter 7.2).

The accumulation of nutrients per unit bole volume varies significantly between clones, and the influences of both crown weight and nutrient concentration are evident (Table 8.18). Clone 579A has the greatest crown weight per bole volume and the greatest weight of most nutrients; but trees of clone 579A have less manganese and more phosphorus than trees of clone 582A due to differences in average concentration. The inconsistent relationships between the clones for the weights of each nutrient per unit bole volume largely negates the objection that bole volume might not closely compare with bole dry weight.

The concentrations of the minor nutrients, manganese and zinc, vary both within and between clones more widely than for the other nutrients assessed, and the totals contained in the crowns of comparable trees vary by more than 100%. For the four major nutrients, the clones with maximum amount of any nutrient had commonly 50% more than the clones with the minimum, but the differences in nutrient content were not consistent between clones for all nutrients; for example, clone 546A accumulated considerable amounts of phosphorus but little calcium. Trees of a clone with considerably greater amounts of a nutrient element are either more efficient in uptake and translocation of that nutrient (presumably a desirable characteristic), or have poorer overall efficiency of utilization (which is presumably undesirable).

Many authors observing differences in nutrient content between provenances, progeny groups or seed lots

have discussed the mechanisms by which the differences might have occurred. Differences in root efficiency to absorb nutrients from the soil or growth medium, the size of the root absorption surface, efficiency of translocation and metabolism, or differential growth responses to other environmental influences, have been postulated (Mergen and Worrall, 1965; Walker and Hatcher, 1965; Steinbeck, 1966; Groves, 1967; Giertych and Fober, 1967), but little evidence of the contribution of any factor to the overall variation has been presented. In most studies of forest trees only small foliage samples have been analysed, so the differences assessed are of concentration only, and not of total amounts accumulated. For the six clones examined the differences between clones are of total crown weight and the nutrients contained in the crown, but differences in the nutrient content of bole and root tissues may increase or to some extent lessen the total nutrient content between similar trees. However, much of the variation in nutrient content assessed can be attributed to variation in branch wood weight between trees either of comparable bole size or of comparable leaf weight.

Differences in nutrient concentration interact with the differences in branch and leaf weight, so the amounts of nutrients accumulated in tree crowns (and probably in the tree) to produce comparable amounts of bole volume or total weight differ markedly between clones. Inevitably these differences influence the silvicultural development of plantations, particularly on low nutrient sites, and eventually the capacity of genotypes to accumulate nutrients may be considered in the selection of seed for the establishment of plantations on such sites. Firstly, considerably more knowledge is needed of the factors contributing to variation in nutrient content and of the correlations between accumulation and requirement, before any variation can be fully utilised either in seed selection or silviculture.

8.5 SUMMARY

Trees of six clones, whose parents were selected for overall phenotypic superiority, have been examined for crown dry weight and nutrient content characteristics. Variations between clones in branch numbers and size were similar to those reported previously. Regressions relating branch leaf or wood weight to branch size differ little between clones; but because of varying branch numbers and average size, linear regressions of total crown weight on bole diameter differ significantly between clones, mainly in the value of the intercept.

The concentrations of six mineral nutrients examined varied between clones, both in overall average for each clone and in small samples of 1-year old leaves. The two estimates of nutrient concentration are not related consistently, and genetic influence in the distribution of nutrients through the crown should be recognised when small foliage samples are used to assess nutrient status of trees.

The crowns of trees with similar bole volume varied markedly in the amounts of each nutrient accumulated, but the variation was inconsistent for either nutrients or clones. The minor nutrients, manganese and zinc, varied most widely between clones but for each nutrient assessed the between-clone variation in the amounts accumulated was at least 40% of the amount in the clone with least. Differences between clones in crown dry weight contributed largely to differences in amounts of nutrients accumulated, but differences in concentration influenced the relationships between clones for each nutrient.

Considerably more information is needed of the factors contributing to variation in nutrient concentration and content of trees before full advantage of such variation can be taken in plantation silviculture.

CHAPTER 9

VARIATION IN SEEDLING REACTION TO NUTRIENT STRESS

Contents

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VARIATION IN SEEDLING REACTION TO NUTRIENT STRESS

9.1 INTRODUCTION

The field study of between-tree variation demonstrated P. radiata trees of contrasting genotype but of similar bole size may accumulate substantially different amounts of some nutrients. The differences in nutrient content may result from differences in crown dry weight or in average concentration of nutrients, but suggest the genotypes differ either in capacity to absorb and translocate nutrients, or in efficiency of utilization of the nutrient concerned. The separate effects are difficult to distinguish under field conditions so an experiment with seedlings was made using controlled conditions of variable nutrient supply.

Most similar studies have compared provenances, and open pollinated seed lots could be compared without intermixing of the genetic composition between seed lots (e.g. Mergen and Worrall, 1965; Giertych and Fober, 1967); sometimes seed lots are intensively screened so maximum variation can be observed (e.g. Shea, et al., 1968). No such precautions could be taken in this study. Cuttings could have been used to preserve the individuals genetic composition and enable the results to be related directly to the field study; however, Fielding (1953) has indicated considerable variation in rooting ability between trees. Any differences in response to nutrient stress between cuttings may result from differing physiological development and capacity to produce an effective root system between clones, unless time was taken to ensure an adequate root system on all plants. There was insufficient time to do this so seedlings were used.

9.2 METHODS

Open-pollenated cones were collected from the original parent tree or from vegetatively reproduced ramets for each of the six clones studied in the 1961 clone block (Chapter 8); clone 954 had been planted in a seed orchard (Fielding, 1964) so a second seed lot was collected of that clone from that source; and two batches of controlled-pollinated seed were made available by Dr L. Pederick of the Victorian Forests Commission. Except for the controlled-pollinated seed lots, seeds were extracted from each cone separately and then combined within mother-tree parents to give about 250 whole seeds per mother-tree seed lot with minimum variation in seed weight both within and between seed lots (Table 9.1). Of the 250 seeds, those with an individual weight within 5% of the batch average weight (usually 70-80 seeds) were selected for germination.

A replicated factorial design was selected so the effects of varying phosphorus supply could be examined for each seed lot. Seeds were pretreated by soaking for 48 hours in water, then washed in dilute hydrogen peroxide as a surface sterilant, and germinated on blotting paper. As each seedling hypocotyl reached about 3 cm, seedlings of each seed lot were placed in nutrient solutions. There was one seedling of each seed lot per tray and 12 trays (replications) for each of four nutrient treatments (Plate 9.1). All seed lots germinated quickly and uniformly, except seed lot 579A which was subsequently abandoned. All other treatments were fully established by December 24, 1967, and surplus seedlings of these were placed in locations marked for seed lot 579A; these surplus seedlings were used to replace the few seedlings that died.

Details of the nutrient solution preparation are given in Appendix 10. All treatments comprised a basic complete nutrient solution without phosphorus, to which phosphorus

PLATE 9.1 Seed source x nutrient stress experiment, immediately after establishment of germinated seedlings in nutrient solutions. Aluminium foil and Sarlon shade cloth (raised) used to minimise light and temperature variation within experiment area, also to eliminate light and reduce temperature of nutrient solutions.

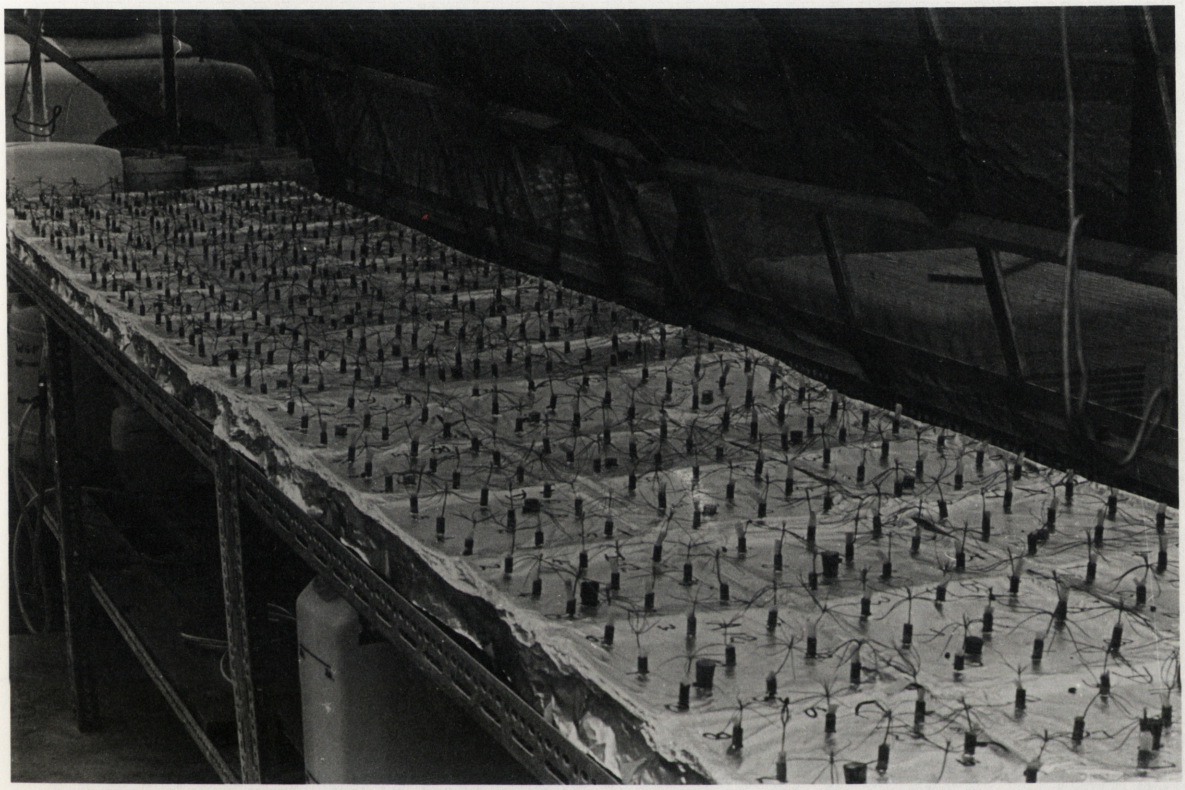


TABLE 9.1 Seed source and weight of seeds used in nutrient experiment

Identification of mother tree	Location of mother tree	Individual Seed weight(gm) (Range used)
546 A	Kowen Plantation, 1961 clone block	0.045 - 0.050
579 A	Kowen Plantation, parent tree	0.027 - 0.030
582 A	Field study, 1961 clone block	0.025 - 0.028
602 A	Field study, 1961 clone block	0.035 - 0.039
605 A	Pierce's Ck. Plantn. Parent tree	0.024 - 0.026
954 (i)	Field study, 1961 clone block	0.038 - 0.042
954 (ii)	Tallaganda seed orchard	0.031 - 0.034
112 A x B.A.21)	Controlled-pollinated	0.043 - 0.046
M.Y.7 x C.R. 55)	seed batches	0.025 - 0.028

was added to give a final concentration in:

Treatment A of 0.5 ppm
Treatment B of 1.5 ppm
Treatment C of 4.0 ppm
Treatment D of 8.0 ppm

It was impossible to aerate the nutrient solutions, but other studies (Will, 1961; P. Barker, unpublished) have shown P. radiata seedlings can be grown for several months in solution without aeration with no apparent deleterious effect provided the solutions are changed regularly. All solutions were changed in this study at 10 day intervals. After 67 days, when the seedlings had grown 15 - 18 cm, the experiment was harvested. All seedlings were separated into tops and roots and the roots were washed quickly in distilled water to remove any nutrient solution from the surface. The seedling tops and roots were oven-dried at 85°C and then analysed for phosphorus content as previously described (Chapter 5.2).

9.3 RESULTS

A summary of treatment means for seedling growth and phosphorus content of eight seed lots at four levels of solution phosphorus are given in Appendix 11. There is an overall increase in seedling dry weight with increasing phosphorus concentration in the nutrient solution, except at the greatest concentration (8 ppm) when the weight of seedlings decreased (Table 9.2). The overall dry weight of seedling tops differed little between seed batches; batches 7 x 55 and 546A had greater average dry weight than all others, suggesting greater average vigour for these seedlings (Table 9.3). However, the overall averages tend to mask the variable relative development of seed lots at each nutrient level.

TABLE 9.2 Dry weight and phosphorus content of seedlings of all batches at varying concentrations of phosphorus in the nutrient solution

LSD = Difference between means required for significance at P = 0.05.
Means coupled by any line are not significantly different.
(96 observations per mean)

SEEDLING					
TOPS		ROOTS		TOTALS	
Treatment	Mean	Treatment	Mean	Treatment	Mean
Dry weight (gms)					
A	0.580	D	0.119	A	0.707
D	0.595	B	0.126	D	0.714
B	0.689	A	0.127	B	0.815
C	0.724	C	0.132	C	0.856
LSD	0.042		0.010		0.048
Phosphorus content (mg)					
A	0.74	A	0.42	A	1.15
B	1.71	C	0.51	B	2.38
D	1.92	B	0.67	D	2.61
C	2.11	D	0.70	C	2.62
LSD	0.18		0.09		0.24
Phosphorus concentration (mg/gm)					
A	1.28	A	3.28		
B	2.50	C	4.04		
C	3.03	B	5.30		
D	3.26	D	6.37		
LSD	0.31		0.74		

TABLE 9.3 Dry weight and phosphorus content of seedlings in each batch over all phosphorus treatments in nutrient solution (48 observations per mean)

LSD = Difference between means required for significance at P = 0.05.
Means grouped within a bracket do not differ significantly

TOPS		ROOTS		TOTAL SEEDLINGS	
Seed batch	Mean	Seed batch	Mean	Seed batch	Mean
Dry weight (gms)					
605 A	0.583	605 A	0.084	605 A	0.667
582 A	0.602	582 A	0.110	582 A	0.713
954 (2)	0.617	112 x 21	0.127	112 x 21	0.745
112 x 21	0.618	7 x 55	0.128	954 (2)	0.762
954 (1)	0.631	546 A	0.129	954 (1)	0.776
602 A	0.649	602 A	0.139	602 A	0.788
7 x 55	0.731	954 (1)	0.145	7 x 55	0.859
546 A	0.744	954 (2)	0.146	546 A	0.873
LSD	0.063		0.015		0.073
Phosphorus content (mg)					
605 A	1.32	605 A	0.39	605 A	1.71
582 A	1.54	954 (1)	0.45	582 A	2.02
954 (2)	1.54	582 A	0.49	954 (1)	2.16
602 A	1.66	602 A	0.56	954 (2)	2.19
954 (1)	1.71	546 A	0.58	602 A	2.22
112 x 21	1.71	954 (2)	0.65	546 A	2.30
546 A	1.72	112 x 21	0.71	112 x 21	2.42
7 x 55	1.75	7 x 55	0.77	7 x 55	2.52
LSD	0.28		0.13		0.37
Phosphorus concentration (mg/gm)					
605 A	2.21	954 (1)	3.10		
546 A	2.36	602 A	4.08		
954 (2)	2.49	582 A	4.45		
602 A	2.50	605 A	4.67		
582 A	2.54	954 (2)	4.74		
7 x 55	2.55	546 A	5.19		
954 (1)	2.73	112 x 21	5.49		
112 x 21	2.77	7 x 55	6.28		
LSD	0.47		1.11		

Seedlings of two batches, 546A and 112A x 21, reached maximum development at 1.5 ppm phosphorus in the nutrient solution, while seedlings of all other batches grew best at 4.0 ppm. Seedlings of all batches grew relatively poorly at 8.0 ppm, but for some the difference in growth between 4.0 and 8.0 ppm was insignificant (Fig. 9.1a).

The concentration of phosphorus in the seedlings increased with increasing phosphorus in the nutrient solution (Table 9.2) although at greater solution concentrations the changes in seedling concentrations were usually insignificant (Fig 9.1b). Only small differences in phosphorus concentration occurred for seedling tops between batches, but the concentrations in the roots differed widely between batches (Table 9.3).

The amounts of phosphorus contained by seedlings of each clone varied greatly (Fig. 9.1c); there was no significant difference between batches for mean phosphorus content at the lowest solution concentration (0.5 ppm), and for most batches the amount of phosphorus contained at 1.5 ppm P was at least double the amount at 0.5 ppm P, but thereafter the pattern of phosphorus accumulation varied. The two batches which grew best at 1.5 ppm P (i.e. batches 546A and 112A x 21) also contained more phosphorus in their tops at 1.5 ppm P than at higher concentrations; in some batches the amount of phosphorus in tops was greatest at the highest solution concentration (8.0 ppm P) whilst for others the amount of phosphorus contained was markedly less at 8.0 ppm P than at 4.0 ppm P (Fig. 9.1c).

The phosphorus requirements of seedlings are best compared by relating the phosphorus contents of the seedling tops to the seedling dry weight at each nutrient solution concentration (Fig. 9.2), only values below the inhibition point are compared because of variable growth and phosphorus content at higher solution concentrations. Both the dry weight and phosphorus content of seedlings 582A and 602A are

FIG. 9-1 DRY WEIGHTS AND PHOSPHORUS CONTENTS OF P.RADIATA SEEDLINGS OF SEVERAL SEED SOURCES GROWN AT FOUR LEVELS OF PHOSPHORUS CONCENTRATION

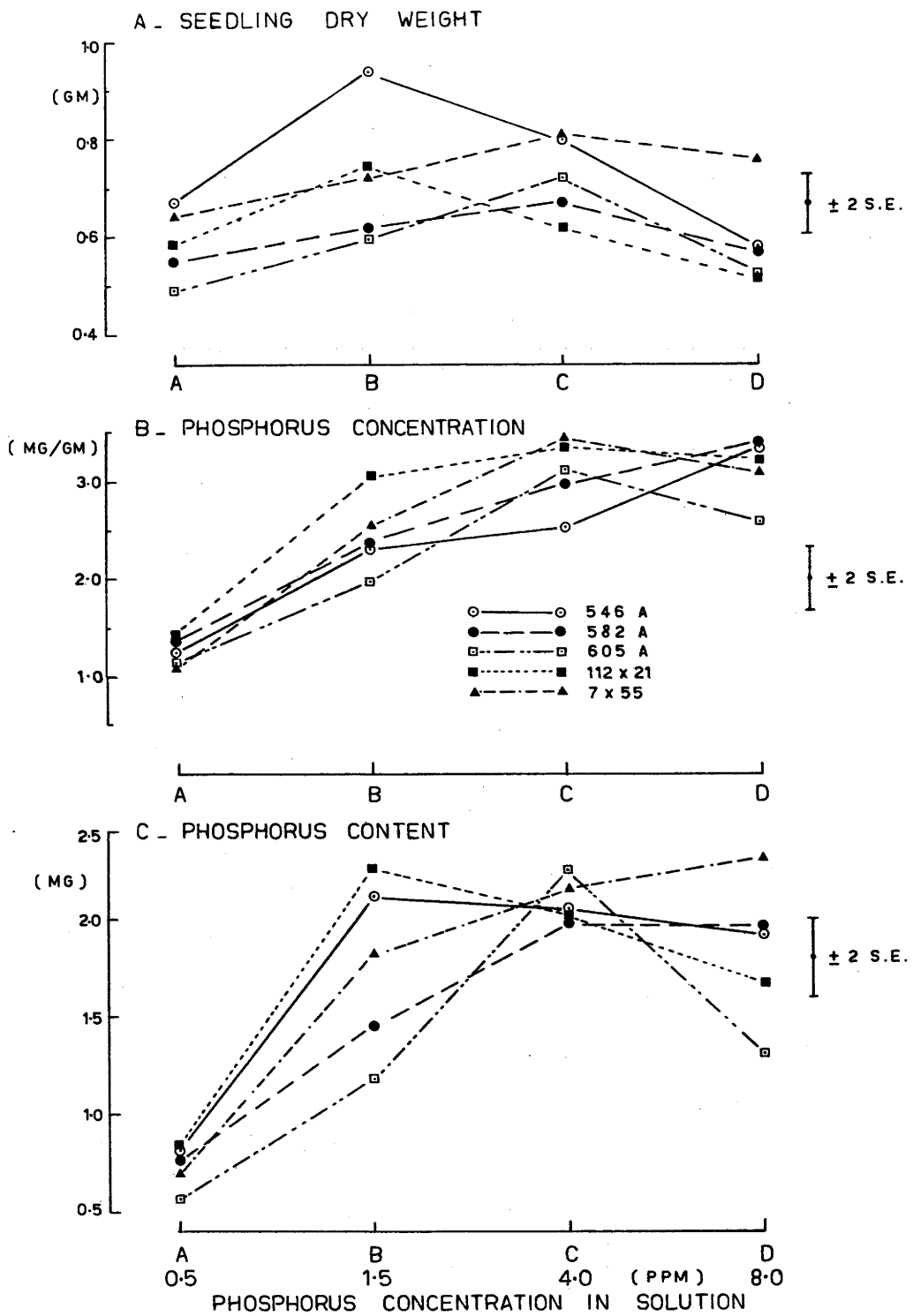
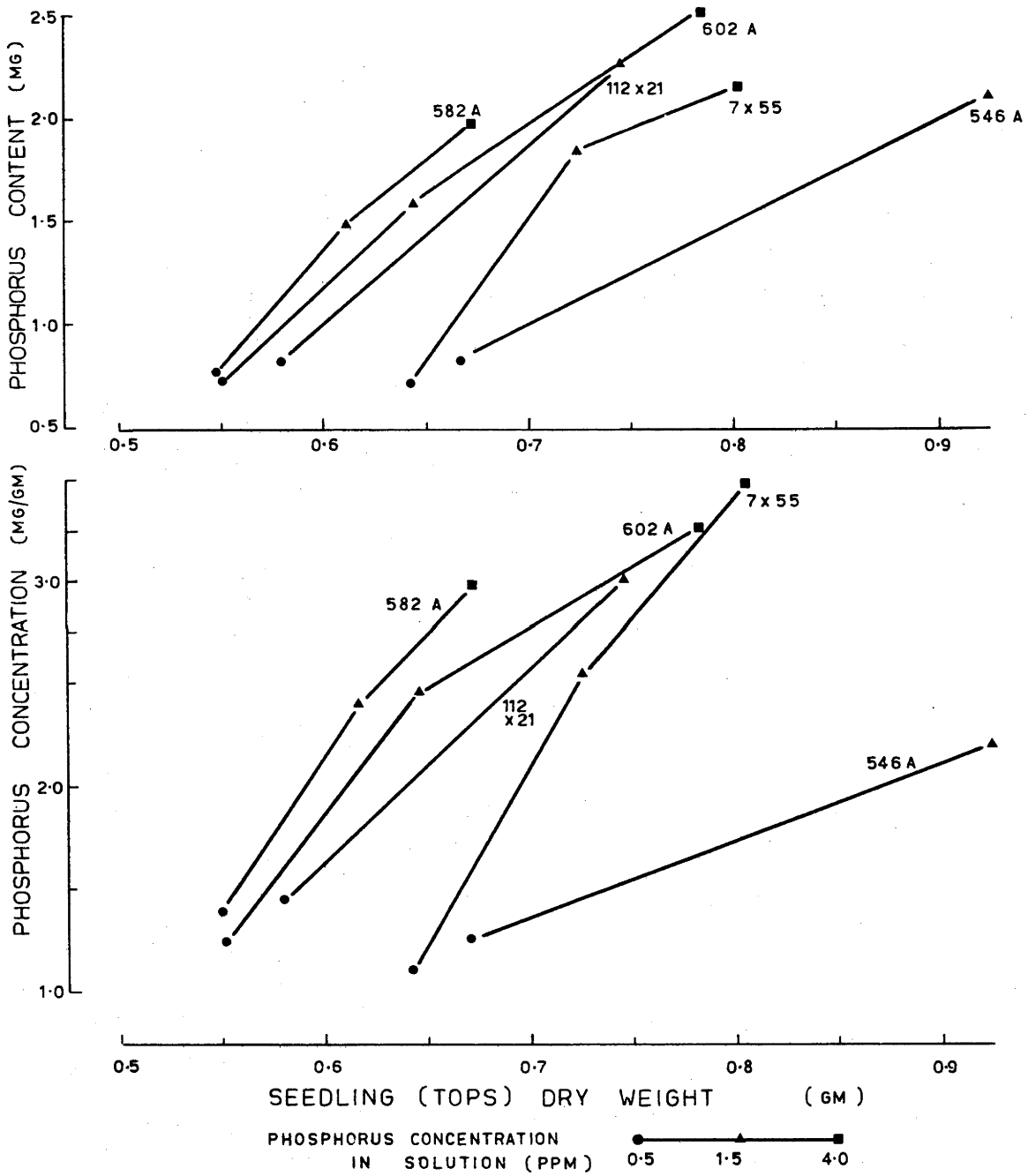


FIG. 9-2 DIFFERENCES BETWEEN SEEDLING BATCHES IN DRY WEIGHT AND PHOSPHORUS CONTENT AT PARTICULAR LEVELS OF SOLUTION PHOSPHORUS



similar at 0.5 and 1.5 ppm phosphorus, but at 4.0 ppm the growth of 602A is substantially greater than of 582A. Neither the amount nor concentration of phosphorus in the roots of those batches vary significantly at any level of solution phosphorus, so it seems seedlings of 602A are naturally more vigorous than of 582A, but this vigour can only be expressed at high phosphorus availability. In contrast, seedlings of 112A x 21 are no more vigorous than those of 602A, but maximum growth of 112A x 21 occurs at a much smaller phosphorus supply level. Similarly, while at 0.5 ppm solution phosphorus seedlings of 546A and 7 x 55 have similar growth and phosphorus content, at higher phosphorus supply (1.5 ppm) the growth of 546A is substantially greater than of 7 x 55, although the concentration in both the roots and tops of those seedlings remain similar.

9.4 DISCUSSION

Seedlings of the several seed lots tested differed in response to varying levels of phosphorus supply. Apart from differences in development at each solution concentration, not all seedlings grew best at the same solution concentration, and seedling groups differed in degree of inhibition of growth at the highest concentration used. Seedling groups also differed in the amounts of phosphorus absorbed at each solution concentration or for a particular dry weight produced.

Considerable variation occurred within each seedling group for both growth and phosphorus content at each treatment level, despite precautions taken to reduce variation. The variation was as great within the controlled-pollinated seedlings as for the open-pollinated seedlings. Although most treatment mean differences discussed are significantly different at $P = 0.05$, means significantly different at $P = 0.10$ could probably also be considered.

Differences in seed weight and phosphorus content could have contributed to the variation in seedling development, but much of the variation is independent of seed size; for example, the two seed lots of clone 954 differ in seed weight but seedling dry weight and phosphorus content means are not significantly different; except at the lowest level of phosphorus supply and seedlings of batches 546A and 7 x 55 were not significantly different in weight or phosphorus content at 0.5 ppm and 4.0 ppm solution phosphorus but differed significantly in both at 1.5 ppm, despite wide differences in seed weight. There is no satisfactory method for eliminating variation in seed weight and composition in studies of this type, or of assessing the effect, particularly since differences may be in either seed coat or endosperm. There is no justification for selecting light seeds from heavy batches to equate seed weights or cutting off part of heavy seeds (Shea, et at., 1968), the results must be interpreted with due consideration to initial variation.

Variation in response of seedlings to nutrient stress has been described for a number of grass and herb species (e.g. Kruckeberg, 1951; Snaydon and Bradshaw, 1962) and more recently for tree species (e.g. Mergen and Worrall, 1965; Groves, 1967), but in each case the species tested was selected over a wide geographic or edaphic range. Groves (1967) has discussed the use of the term "edaphic ecotype" which has been used to describe within-species variation in reaction to site and nutrient supply. Although the variation observed in this study is similar to that reported previously the seedling groups cannot be regarded as ecotypes (Chapter 8).

The amounts of phosphorus accumulated in the tops of seedlings of each seed lot can be generally related to the phosphorus content of the parent trees (Table 9.4). At sub-optimal levels of phosphorus supply (as probably exist

TABLE 9.4 Relative amounts of phosphorus in open-pollinated *P. radiata* seedlings and vegetatively propagated trees of the same parentage

Average phosphorus content in seedling tops at : 0.5 ppm P in the nutrient solution		Average phosphorus content in seedling tops at : 1.5 ppm P in the nutrient solution		Average P concentration in 1-year old leaves (Table 8.11)		Weight of P in crowns of trees per unit bole volume (Table 8.18)	
Seed lot	P (mg)	Seed lot	P (mg)	Clone	P (%)	Clone	P (kg/cu m)
605A	0.55	605A	1.17	605A	0.14	605A	0.39
954(2)	0.64	582A	1.45	602A	0.15	954	0.40
602A	0.68	602A	1.59	582A	0.16	582A	0.47
582A	0.76	954(1)	1.62	546A	0.17	602A	0.49
546A	0.82	954(2)	1.68	954	0.18	546A	0.49
954(1)	0.88	546A	2.12				

under field conditions, see Chapter 8), seedlings of seed lot 605A contain least phosphorus and of seed lots 954 and 546A contain most phosphorus, and this relative difference also pertains in the foliage of the 1961 clones. The relatively low phosphorus content of seedlings of seed lot 582A and of 954 (2) at 0.5 ppm phosphorus may in part be due to lower seed weight and phosphorus content, but these effects are largely negated at higher levels of phosphorus availability. Thus the results from the studies in plantation trees and the seedlings are in general agreement. It seems both seedlings and trees with the genetic composition of parent 546A can accumulate and utilise phosphorus at low levels of availability more efficiently than other types examined. In contrast, clone 605A seems less able to accumulate phosphorus and at low levels of availability this has restricted seedling growth. Seedlings of 605A also have considerably less phosphorus in the roots, but this could be due to poorer root development as a result of restricted photosynthesis. It is still impossible to determine whether differences in nutrient accumulation are due to differences in root uptake, in translocation, or in efficiency of utilization.

Results for plantation trees, similar to those discussed above, have recently been reported for P. radiata in New Zealand (Hinds, 1968), the relative growth of several clones of P. radiata was consistent for three planting sites, but at another site where phosphorus is deficient the "clonal differences are extreme and bear little or no relationship to those on the other three sites". Similar results have been observed elsewhere (Pawsey, 1968). In view of the extreme range in fertility of sites on which P. radiata plantations are established in Australia, variation in nutrient requirements and utilization by apparently similar phenotypes, and the consequent differences in relative development of genotypes on contrasting soils, are likely to be of considerable importance in P. radiata silviculture.

9.5 SUMMARY

The growth and phosphorus content of P. radiata seedlings from eight seed lots grown at four levels of phosphorus availability were examined. The seed lots were mainly open-pollinated and from clones examined previously as plantation trees, but two controlled-pollinated seed lots were included.

Seedling dry weight and phosphorus content differed significantly between seed lots at all except the lowest level of solution phosphorus. Seedlings from different parents did not all grow best at the same level of availability, suggesting a variable requirement of phosphorus for optimal growth. The results could be generally related to the phosphorus concentration in 6 year old clones of the same parentage, so the results from the seedling study support the previous conclusion, that P. radiata genotypes vary in capacity to accumulate and utilise mineral nutrients. More intensive study of the physiology of nutrient movement and utilization is necessary before the factors contributing to the overall variation between genotypes can be differentiated.

GENERAL DISCUSSION

GENERAL DISCUSSION

"The basis of plantation silviculture in Australia is changing rapidly and radically, ...silviculture as an art is being supplanted by a new silviculture, mechanised and cost conscious" (Shepherd, 1968a). Yet forest plantations increasingly need to be considered as biological units because of the increasing demand for greater production, diversity of product, and uniformity of raw material. Silvicultural considerations must develop from an understanding of physiological processes concerned in production, so the biological unit can be manipulated to provide the multi-requirements of forest policy.

Primary production within a forest stand is a balance between overall photosynthesis and total respiration, and the crop removed is usually only a part of primary production. The silviculturalist must select for planting the tree species most suited to the environment and to future markets, whilst recognising the possibilities of site modification to suit the physiological characteristics of the plant. During a forest rotation the stand structure may be modified from time to time for an optimal balance between photosynthesis and respiration, and for optimal distribution of total production into the crop material.

Little is known of the effect of silvicultural treatment on total respiration. Satoo (1968) estimated that for a 16.6 m tall stand of Cinnamomum the annual net production above ground, leaf respiration, and respiration from non-photosynthetic tissues were each about 15 m tons per ha. The annual net production in 12 - year old, 16 m tall P. radiata stands was also estimated to be 15 m tons per ha, and whilst the photosynthetic capacity of the stand probable decreases slowly after that age (Chapter 2.3.3), total

respiration will increase as the amount of non-photosynthetic respiring tissue increases. The photosynthesis: respiration ratio decreases with stand age (Hosner and Madgwick, 1967) and although because of the longer growing season, foliar respiration may be less for P. radiata than estimated by Satoo, total respiration probably becomes important in older P. radiata stands.

The factors influencing total respiration are not well-known, but respiration may be decreased by increasing the duration of photosynthesis, or by lessening the surface area of non-photosynthesising material. Within a pine stand the duration of photosynthesis might be increased by improving soil conditions or adjusting the canopy configuration. Branch and bole surface area per unit ground area both vary with tree stocking; in young plantations branch size may be limited by dense tree stocking, but in older stands respiration might be minimised using the smallest number of even - sized trees commensurate with full canopy cover.

Total photosynthesis is determined by two factors, viz., the quantity of leaves and their photosynthetic efficiency (Satoo, 1967b). For agricultural crops, nutrient stress may cause reduced productivity primarily, or even exclusively, through a reduction in leaf area, except at extreme nutrient stress (Watson, 1952). In young forest stands the quantity of leaves per tree or per unit area increases with improved soil nutrient status (Keay et al., 1968), and the relative growth rate is also greater. After tree canopies fully close, leaf weights (and consequently leaf area indices) may vary substantially between stands of comparable site quality (Chuong, 1967), but are not closely related to site quality (Chapter 2.4.3). The hypotheses of Moller (1947), that leaf weight is independent of site, and both leaf weight and total production are relatively independent of stand density, have been generally accepted,

although for some shade tolerant species leaf weights might increase slightly with increasing stand density (Baskerville, 1965). Satoo (1967b) attributed the minimal effects of many environmental factors on stand leaf weight to the over-riding influence of light in determining the quantity of leaves. Leaf weights possibly vary as much between stands of comparable site quality as of contrasting site quality, and Madgwick (1962) has discussed the reasons for differences in stand leaf weight within species. It seems for P. radiata differences in site influence overall leaf efficiency more than total leaf amounts (Chapter 4), consequently leaf efficiency should be examined closely.

Photosynthesis per unit leaf area per annum (overall leaf efficiency) is determined by the efficiency of the photosynthetic process (i.e. amounts of carbohydrates assimilated per unit of time), the diurnal and seasonal duration of the process, and leaf longevity. The initiation and cessation of photosynthesis are determined by the interaction of many fluctuating environmental influences, as temperature, humidity and light intensity, and the relatively more stable edaphic influences (Wood, 1968), so the duration of photosynthesis, both diurnally and seasonally, is probably reduced when additional stresses are imposed. Whilst not all nutrients are involved directly in photosynthesis, deficiencies for any will eventually impose stresses on the process (Nason and McElroy, 1963). Consequently the alleviation of nutrient stress by fertilizer addition may increase the duration of photosynthesis in forests.

The efficiency of the photosynthetic process has been considered as relatively independent of moderate changes in leaf nutrient status (Watson, 1956). However, the various nutrients, having differing locations of essential activity, may differ in the effects of deficiency on photosynthetic processes. Bouma (1967) has indicated leaf photosynthetic

activity might be directly responsive to moderate changes in the availability in nutrients, particularly changes in phosphorus and sulphur status.

Overall leaf efficiency may change with stand age (Chapter 4) because of changes in intrinsic efficiency associated with tree maturity, or changes in environmental limitations as the trees grow. For many tree species, leaves change in morphology from a juvenile to mature form as the tree ages. Wood (1968) indicated anatomical differences between leaves of successive ages in young P. radiata trees, and the extent to which changes in nutrient concentrations in leaves with tree age (Chapter 5.3), particularly for magnesium, result from increasing leaf maturity is unknown.

Trees may vary genetically in photosynthetic capacity (Chapter 8), although the differences are most likely in the seasonal course of photosynthesis (Zelawski, 1967), and this in turn may be influenced by nutrient supply.

An improved understanding of the physiology of nutrient accumulation and utilization in trees may assist in the selection of planting stock for nutritionally poor sites. Trees differ markedly according to genotype in nutrient requirements for optimal growth (Chapter 8). Whilst considerable research is needed before the genetic variability can be used to reduce the incidence of nutritional deficiencies in plantations, some advances can be made immediately. For example, trees with small branches are desirable for various reasons, to ensure small knots in the finished board, ease of pruning, etc. However, branch size also influences the proportion of total production in useable crop components, determines canopy shape and so has silvicultural implications, and trees with many large branches probably accumulate excessive nutrients. Similarly, trees with thin bark possibly have lesser nutrient requirements and with harvesting less nutrient would be

removed from the site. Within the present tree improvement programmes, the concentrations of nutrients can be assessed and compared for clones of genotypes selected for seed production as a guide to further experimentation. The relative reactions of genotypes to particular edaphic environments can be assessed, for example variable growth observed of clones in a seed orchard has been attributed to a differential response between clones to low boron availability (Dr S.W. Gentle, pers. comm.)

Facets of the present study have illustrated the importance of an appreciation of the nutritional characteristics of the forest stand in many silvicultural considerations. In localities where nutrient deficiencies may be experienced because of restricted availability of one or several nutrients within the tree root zone, treatments will be advantageous which either increase the availability of nutrients or reduce the rate of nutrient requirement at any particular time or over the whole rotation. For example, the leaching of certain nutrients from the site in drainage water may be appreciable at any time but is accellerated following clear-felling for plantation establishment (e.g. Bormann, et al., 1967). Leaching of phosphorus and potassium is likely to be extreme on freely draining sandy soils where reserves of these nutrients might already be small. In such situations if a second rotation pine crop was established by natural regeneration, as described by Shepherd (1968b), nutrients released from litter of the first crop might contribute substantially to the early requirements of the second crop. Other techniques for retaining the accumulated nutrients within the living trees, such as pruning only dead or dying branches to ensure full redistribution of nutrients, may be desirable particularly since pruning is often done when the rate of requirement for nutrients in new growth is greatest.

Little attention has been given, either in this study or in Australian forest research generally, to the growth of roots, although root development is certainly important to total stand production (Grose 1968). Detailed studies are needed to provide data on the nature of root growth, the effects on growth of various environmental factors and of such operations as thinning and fertilizer addition, so the more fundamental studies of root physiology and nutrient transfer from soil to plant can be related to forest management practice.

Clearly, there is a need for further research into the processes of forest growth. These studies emphasise the potential value of such data.

CONCLUSIONS

CONCLUSIONS

Techniques for determining the dry weight of the trees in even-aged forest stands have been investigated as a basis for studies of the factors influencing dry weight accumulation and the circulation of mineral nutrients in plantations.

Unit area methods of stand dry weight assessment were unsatisfactory because of the irregular distribution of organic matter spatially. Average tree methods gave relatively accurate estimates of component and total dry weight, but because the largest trees were about four times the linear dimensions and more than fifty times the weight of the smallest trees, a large number of trees need to be sampled before acceptable statistical limits could be attributed to any weight estimates. Since component and total tree weights generally increased with bole size, regression analysis methods of stand weight estimation proved most satisfactory. The stand dry weights of the major components and total trees in the study area could be estimated to within 10% of the actual weight from a sample of only 10 trees. The distributions of the minor components, such as dead branches and female cones, were so irregular these could only be estimated accurately if only the trees having them are considered. The inclusion of linear dimensions other than bole size did not improve the size: weight relationships, but this could have resulted from insufficiently precise measurement.

In the study area the single tree was considered as the sample unit, and subdivided by components. In future consideration might be given to regarding each component independently. For instance, in a later study (Part III) stand leaf and branch dry weights were accurately estimated by taking the single branch as the sample unit.

The accumulation of organic dry weight in the several above-ground layers of a pine plantation has been described. Initially, weed growth was important but after the third year the growth of non-pine vegetation decreased because of competition from the pine trees and the cleaning operations of management. The rate of crown expansion increased greatly up to canopy closure, and in the sixth year foliage dry weight increased by 8 m tons per ha. After canopy closure the annual increase in foliage weight was only 4 m tons per ha, so the weight of foliage was greatest and so also was the stand photosynthetic capacity, at the time of canopy closure. The greatest rate of bole wood production was 12m tons per ha between 7 and 9 years, but thereafter bole wood production was about 10 m tons per ha per annum. Total production was about 33 and 20 m tons per ha per annum immediately before and after canopy closure, respectively.

The overall rate of nutrient accumulation followed the general pattern of dry weight accumulation, but important differences were observed between the nutrients according to the relative concentrations of each in the various tree components, and the rate of redistribution both within the tree and externally through litter fall. For example, after canopy closure the phosphorus requirements for bole wood production are small, and much of the phosphorus accumulated in new canopy growth each year results from internal redistribution from the older material and particularly from older leaves before their abscission. In contrast, calcium accumulates slowly in bole wood, but is also continually accumulated in older canopy material so the requirements after canopy closure are relatively great. Some of the silvicultural implications have been discussed of the differences in rate of accumulation with time for each nutrient, and the differences in distribution and movement between nutrients.

During this study large differences were observed in the distributions of weight, particularly through the canopy, and of nutrient element contents of otherwise apparently similar trees. A field study of clonal trees showed between - tree variation in nutrient content resulted from differences in branch wood dry weights and to a lesser extent in foliage dry weights and from differences in the concentrations of nutrients. Variations in both crown dry weight and nutrient concentrations were under strong genetic influence. A seedling glasshouse study indicated trees differ genetically not only in the amounts of nutrients accumulated but also in the site requirements for optimal growth. Further research is needed before the full implications of such variation can be fully understood.

REFERENCES

Arita, M., and K. Tomita. 1964. The effect of seed collection from trees in a natural forest of Cryptomeria japonica on the crown-types of their progenies. J. jap. For. Soc. 46: 205-207

Attiwill, P.M. 1962. Estimating branch dry weight and leaf area from measurements of branch girth in Eucalyptus. Forest Sci. 8: 132-141

Attiwill, P.M. 1966 a. A method for estimating crown weight in Eucalyptus, and some implications of relationships between crown weight and stem diameter. Ecology 47: 795-804

Attiwill, P.M. 1966 b. The chemical composition of rainwater in relation to cycling of nutrients in mature eucalyptus forest. Pl. Soil 24: 390-406

Attiwill, P.M. 1968. The loss of elements from decomposing litter. Ecology 49: 142-145

Attiwill, P.M., and J.D. Ovington. 1968. Determination of forest biomass. Forest Sci. 14: 13-15

Baskerville, G.L. 1965 a. Dry-matter production in immature balsam fir stands. Forest Sci. Monogr., Wash. No. 9, 42 pp

Baskerville, G.L. 1965 b. Estimation of dry weight of tree components and total standing crop in conifer stands. Ecology 46: 867-869

Baskerville, G.L. 1966. Dry-matter production in immature balsam fir stands: roots, lesser vegetation, and total stand. Forest Sci. 12: 49-53

Baur, G.N. 1959. Responses to Phosphate, Barcoongere Plantation, N.S.W. Aust. For. 23: 12-18

Bazilevič, N.I., and L.E. Rodin. 1966. The biological cycle of nitrogen and ash elements in plant communities of the tropical and subtropical zones. For. Abstr. 27: 357-368

Beadle, N.C.W., and G.I. White. 1968. The mineral contents of the tree trunks of some Australian woody plants. Proc. Ecol. Soc. Aust. (in press)

Beaton, J.D., G. Brown, R.C. Spear, I. MacRae, W.P.T. McGhee, A. Moss, and R. Kosick. 1965. Concentrations of micronutrients in foliage of three coniferous tree species in British Columbia. Proc. Soil Sci. Soc. Am. 29: 299-302

Beaton, J.D., A. Moss, I. MacRae, J.W. Konkin, W.P.T. McGhee, and N. Kosick. 1965. Observations on foliage nutrient content of several coniferous tree species in British Columbia. For. Chron. 41: 222-236

Bormann, F.H., G.E. Likens, D.W. Fisher, and R.S. Pierce. 1967. Nutrient loss accelerated by clear cutting of a forest ecosystem. In "Symposium on primary productivity and mineral cycling in natural ecosystems". ed H.E. Young. Univ. Maine Press. pp 187-196

Bouma, D. 1967. Growth changes of subterranean clover during recovery from phosphorus and sulphur stresses. Aust. J. biol. Sci. 20: 51-66

Bray, J.R. 1962. Root production and the estimation of net productivity. Can. J. Bot. 41: 65-72

Bray, J.R., and E. Gorham. 1964. Litter production in forests of the world. Adv. ecol. Res. 2: 101-157

Brewer, R. 1955. In "The Australian Capital Territory as a region". ed H.L. White. Halstead Press, Sydney. pp 44-47

Burger, H. 1929. Holz, Blattmenge und Zuwachs. 1. Die Weymouthsfohre. Mitt. Schweiz. ZentAnst. forstl. Versuchsw. 15: 243-292

Burger, H. 1936. Holz, Blattmenge und Zuwachs. 2. Die Douglasie. Ibid. 19: 21-72

Burger, H. 1940. Holz, Blattmenge und Zuwachs. 4. Ein 80 jahriger Buchenbestand. Ibid. 21: 307-348

Cable, D.R. 1958. Estimating surface area of ponderosa pine foliage in central Arizona. Forest Sci. 4: 45-49

Campbell, R.K. 1961. Phenotypic variation and some estimates of repeatability of branching characteristics of Douglas fir. Silvae Genet. 10: 109-118

Carlisle, A., A.H.F. Brown, and E.J. White. 1967. The nutrient content of rainfall and its role in the forest nutrient cycle. Proc. 14th Congr. int. Un. Forest Res. Org. Munich, 1967 Sect. 21: 145-158

Cole, D.W., S.P. Gessel, and S.F. Dice. 1967. Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second-growth Douglas-fir ecosystem. In "Symposium on primary productivity and mineral cycling in natural ecosystems". ed H.E. Young. Univ. Maine Press. pp 197-232

Chuong, P.H. 1967. Forest site productivity. Unpub. B.Sc. (Hons.) Thesis Aust. National Univ. Canberra.

Cummings, W.H. 1941. A method for sampling the foliage of a silver maple tree. J. For. 39: 382-384

Curlin, J.W. 1967. Clonal differences in yield response of Populus deltoides to nitrogen fertilization. Proc. Soil Sci. Soc. Am. 31: 276-279

Dormer, K.J. 1965. Correlations in plant development: general and basic aspects. In "Encyclopedia of Plant Physiology", 15: 452-491

Duvigneaud, P., and S. Denaeyer-DeSmet. 1967 Biomass, productivity and mineral cycling in deciduous forests in Belgium. In "Symposium on primary productivity and mineral cycling in natural ecosystems". ed H.E. Young. Univ. Maine Press. pp167-186

Ehrenburg, C.E. 1966. Parent-progeny relationships in Scots pine. Results from three progeny tests with plus and minus tree progenies in southern Sweden. Stud. for. Suecica Nr 40

Epstein, E., and R.L. Jefferies. 1964. The genetic basis of selective ion transport in plants. A. Rev. Pl. Physiol. 15: 169-184

Fielding, J.M. 1953. Variation in Monterey pine. Bull. Commonw. For. Timb. Bur. Aust. No 31

Fielding, J.M. 1954. Methods of raising Monterey pine from cuttings in the open nursery. Bull. Commonw. For. Timb. Bur. Aust. No 32

Fielding, J.M. 1955. The seasonal and daily elongation of the shoots of Monterey pine and the daily elongation of the roots. Leafl. Commonw. For. Timb. Bur. Canberra No 75

Fielding, J.M. 1960. Branching and flowering characteristics of Monterey pine. Bull. Commonw. For. Timb. Bur. Aust. No 37

Fielding, J.M. 1961. Provenances of Monterey and bishop pines. Bull. Commonw. For. Timb. Bur. No 38

Fielding, J.M. 1964. Notes on a Monterey pine seed orchard on Tallaganda State Forest in New South Wales. Aust. For. 28: 203-206

Fielding, J.M., and A.G. Brown. 1960. Variations in the density of the wood of Monterey pine from tree to tree. Leafl. Commonw. For. Timb. Bur. Canberra No 77

Fielding, J.M., and A.G. Brown. 1961. Tree-to-tree variations in the health and some effect of superphosphate on the growth and development of Monterey pine on a low-quality site. Leafl. Commonw. For. Timb. Bur. Canberra No 79

Gentle, S.W., J.L. Henry, and K. Shepherd. 1962. The application of basal area control to thinning of Pinus radiata plantations in New South Wales. Proc. 8th Br. Commonw. For. Conf.

Gentle, S.W., and F.R. Humphreys. 1967 Experience with phosphatic fertilizers in man-made forests of Pinus radiata in New South Wales. Paper to "Symposium on Man-made Forests". Canberra, 1967

Gerhold, H.D. 1959. Seasonal variation of chloroplast pigments and nutrient elements in the needles of geographic races of Scotch pine. Silvae Genet. 8: 113-123

Gerloff, G.C. 1963. Comparative mineral nutrition of plants. A. Rev. Pl. Physiol. 14: 107-124

Giertych, M., and H. Fober. 1967. Variation among Norway spruce of Polish provenances in seedling growth and nitrogen uptake. Proc. 14th Congr. int. Un. Forest Res. Org., Munich, 1967 Sect. 22: 536-550

Grose, R.J. 1968. Forest management and silviculture and their effect on forest productivity. Crown and root relationships in white spruce plantations. Proc. 5th Conf. Inst. For. Aust. Perth, 1968

Groves, R.H. 1967. Within-species variation in the growth and nutrition of Eucalyptus cladocalyx. Aust. J. Bot. 15: 161-173

Guha, M.M., and R.L. Mitchell. 1965. The trace and major element composition of the leaves of some deciduous trees. 1. Sampling techniques. Pl. Soil 23: 323-338

Guha, M.M., and R.L. Mitchell. 1966. The trace and major element composition of the leaves of some deciduous trees. 2. Seasonal changes. Pl. Soil 24: 90-112

Hall, M.J., and H.M. Purnell. 1961. Potassium deficiency in Pinus radiata (Don) in eastern Victoria. Aust. For. 25: 111-115

Hall, M.J., and M. Raupach. 1963. Foliage analyses and growth responses in Pinus radiata (D. Don) showing potassium deficiencies in eastern Victoria. Appita 17: 76-84

Hamilton, C.D. 1964. The effect of Monterey pine (Pinus radiata D.Don) on the properties of natural eucalyptus forest and woodland soils. Unpub. M.Sc. Thesis. Univ. West Australia

Hearman. J. 1938. Minor nutrients and the pine. Aust. For. 3: 24-27

Hewitt, E.J. 1963. The essential nutrient elements: requirements and interactions in plants. In "Plant Physiology, 3.Inorganic nutrition of plants." Academic Press, London. pp 137-360

Hinds, H.V. 1968. Report for the period 1 January to 31 December, 1967. Forest Res. Inst. N.Z. Forest Serv. Wellington 88pp

Hosner, J.F., and H.A.I. Madgwick. 1967. Concepts of tree growth. Proc. 14th Congr. int. Un. Forest Res. Org., Munich, 1967 Sect. 26: 353-361

Humphreys, F.R. 1958. The occurrence of rutin in the extraction of rutin from the foliage of commercially important N.S.W. species. Rep. Div. Wood Tech. For. Comm. N.S.W. Project C 12

Humphreys, F.R. 1965. Nutrient status of pine plantations in central New South Wales. Appita 18: 111-121

Humphreys, F.R., and S.W. Gentle. 1968. Exotic forestry on soils of low natural fertility. ANZAAS. 1968

Humphreys, F.R., and J. Kelly. 1962. The variation of phosphorus content in Pinus elliottii foliage. Aust. For. 26: 77-86

Huxley, J.S. 1932. Problems of relative growth. Methuen. London

Jacobs, M.R. 1962. The effect of grade of thinning on growth, ring width and thinning yield in plantations of Pinus radiata in Australia. Leafl. Commonw. For. Timb. Bur. Canberra No 84

Jeffers, J.N.R. 1960. Experimental design and analysis in forest research. Almqvist and Wiksell. Stockholm. 172 pp

Keay, J., A.G. Turton, and N.A. Campbell. 1968. Some effects of nitrogen and phosphorus fertilization of Pinus pinaster in Western Australia. Forest Sci. (in press)

Keeves, A. 1966. Some evidence of loss of productivity with successive rotations of Pinus radiata in the south-east of South Australia. Aust. For. 30: 51-63

Kira, T., and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jap. J. Ecol. 17: 70-87

Kittredge, J. 1944. Estimation of the amount of foliage of trees and stands. J. For. 42: 905-912

Kozlowski, T.T., and C.H. Winget. 1964. The role of reserves in leaves, branches, stems, and roots on shoot growth of red pine. Am. J. Bot. 51: 522-529

Kramer, P.J. 1959. Physiological aspects of research on inorganic nutrition of trees. In "Mineral nutrition of trees." Duke Univ. Sch. For. Bull. 15: 83-88

Kruckeberg, A.R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. Am. J. Bot. 38: 408-419

Lewis, N.B. 1962. Some effects of thinning on value production. Aust. For. 26: 33-34

Leyton, L. 1956. The relationship between the growth and mineral composition of the foliage of Japanese larch (Larix leptolepis, Murr.). Pl. Soil 7: 167-177

Leyton, L., and K.A. Armson. 1955. Mineral composition of the foliage in relation to the growth of Scots pine. Forest Sci. 1: 210-218

Likens, G.E., F.H. Bormann, N.M. Johnson, and R.S. Pierce. 1967. The calcium, magnesium, potassium, and sodium budgets for a small forested ecosystem. Ecology 48: 772-785

Loomis, R.M., R.E. Phares, and J.S. Crosby. 1966. Estimating foliage and branchwood quantities of shortleaf pine. Forest Sci. 12: 30-39

Lowry, G.L., and P.M. Avard. 1965. Nutrient content of black spruce needles. 1. Variations due to crown position and needle age. Woodl. Res. Index Pulp Pap. Res. Inst. Can. No 171

Madgwick, H.A.I. 1962. Studies in the growth and nutrition of Pinus resinosa Ait. Unpub. Ph.D. Thesis Syracuse. New York

Madgwick, H.A.I., and J.D. Ovington. 1959. The chemical composition of precipitation in adjacent forest and open plots. Forestry 32: 14-22

Marchenko, A.I., and E.M. Karlov. 1962. Mineral exchange in spruce forests of the Northern Taiga and Forest Tundra in Arkhangelsh Oblast. Soviet Soil Sci. 1963: 722-734

Mergen, F., and J. Worrall. 1965. Effect of environment and seed source on mineral content of Jack pine seedlings. Forest Sci. 11: 393-400

Metz, L.J. and C.G. Wells. 1965. Weight and nutrient content of the aboveground parts of some loblolly pines. Res. Pap. U.S. For. Serv. Stheast. For. Exp. Sta. SE-17

Metz, L.J., C.G. Wells, and B.F. Swindel. 1966. Sampling soil and foliage in a pine plantation. Proc. Soil Sci. Soc. Am. 30: 397-399

Miller, R.B. 1961. The chemical composition of rainwater at Taita, New Zealand, 1956-1958. N.Z. Jl Sci. 4: 844-853

Miller, R.B. 1963. Plant nutrients in hard beech. 1. The immobilization of nutrients. N.Z. Jl Sci. 6: 365-377

Miller, R.B., and R.B. Hurst. 1957. The quantity and nutrient content of hard beech litter. N.Z. For. Res. Notes 8

Miller, W.F. 1966. Annual changes in the foliage nitrogen, phosphorus, and potassium levels of loblolly pine (Pinus taeda L.) with site and weather factors. Pl. Soil 24: 369-378

Moller, C.M. 1947. The effect of thinning, age, and site on foliage, increment, and loss of dry matter. J. For. 45: 393-404

Nason, A., and W.D. McElroy. 1963. Modes of action of the essential mineral nutrients. In "Plant Physiology, 3.Inorganic nutrition of plants". Academic Press, London. pp 451-536

New South Wales Forestry Commission. 1962. Unpub. Report on management investigations. Red Hill, Billapaloola and Wee Jasper State Forests

Northcote, K.H. 1965. A factual key for the recognition of Australian soils. Rep. Div. Soils C.S.I.R.O. Aust. 2nd edn. Rep 2/65

Northcote, K.H. 1966. Atlas of Australian soils. Explanatory data for Sheet 3. Rep. Div. Soils C.S.I.R.O. Aust. Melbourne Univ. Press

Olsen, J.S. 1967. Report to Ecol. Soc. Study Committee, by the sub-committee on Chemical cycles in Ecological Systems. Ecol. Soc. Am.

Orman, H.R., and G.M. Will. 1960. The nutrient content of Pinus radiata trees. N.Z. Jl Sci. 3: 510-522

Ovington, J.D. 1956. The composition of tree leaves. Forestry 29: 22-28

Ovington, J.D. 1957. Dry matter production by Pinus sylvestris L. Ann. Bot. N.S. 21: 287-314

Ovington, J.D. 1959 a. Mineral content of plantations of Pinus sylvestris L. Ann. Bot. N.S. 23: 75-88

Ovington, J.D. 1959 b. The circulation of minerals in plantations of Pinus sylvestris L. Ann. Bot. N.S. 23: 229-239

Ovington, J.D. 1959 c. The calcium and magnesium contents of tree species grown in closed stands. New Phytol. 58: 164-175

Ovington, J.D. 1963. Flower and seed production. A source of error in estimating woodland production, energy flow and mineral cycling. Oikos 14: 148-153

Ovington, J.D. 1965. Organic production, turnover and mineral cycling in woodlands. Biol. Rev. 40: 295-336

Ovington, J.D., and H.A.I. Madgwick. 1959 a. The growth and composition of natural stands of birch. 1. Dry-matter production. Pl. Soil 10: 271-283

Ovington, J.D., and H.A.I. Madgwick. 1959 b. The growth and composition of natural stands of birch. 2. The uptake of mineral nutrients. Pl. Soil 10: 389-400

Ovington, J.D., and H.A.I. Madgwick. 1959 c. Distribution of organic matter and plant nutrients in a plantation of Scots pine. Forest Sci. 5: 344-355

Pawsey, C.K. 1959. The seasonal fall of litter under Monterey pine in the South East of S. Aust. Inst. Forester Aust. Newsl. 2(4): 16-17

Pawsey, C.K. 1968. Increased productivity of pines through vegetative propagation. Proc. 5th Conf. Inst. For. Aust. Perth, 1968

Piper, C.S. 1944. Soil and plant analysis. Univ. Adelaide. Adelaide, Aust. 368 pp

Raupach, M. 1967 a. Soil and fertilizer requirements for forests of Pinus radiata. Adv. Agron. 19: 307-353

Raupach, M. 1967 b. The growth of radiata pine on lateritic soils at Second Valley, South Australia. Aust. For. 31: 246-262

Remezov, N.P. 1961. Decomposition of forest litter and the cycle of elements in an oak forest. Soviet Soil Sci. 1961 (7): 703-711

Rodin, L.E., and N.I. Bazilevič. 1966. The biological productivity of the main vegetation types in the northern hemisphere of the old world. For. Abstr. 27: 369-372

Rogerson, T.L. 1964. Estimating foliage on loblolly pine. Res. Note U.S. For. Serv. Southern For. Expt. Sta. SO-16

Roy, D.F. 1966. Silvical characteristics of Monterey pine (Pinus radiata D. Don). Res. Pap. U.S. For. Serv. Pacific Southwest Expt. Sta. PSW-31

Rutter, A.J. 1955. The relation between dry weight increase and linear measures of growth in young conifers. Forestry 28: 125-135

Rutter, A.J. 1957. Studies in the growth of young plants of Pinus sylvestris L. 1. The annual cycle of assimilation and growth. Ann. Bot. N.S. 21: 399-426

Satoo, T. 1962. Notes on Kittredge's method of estimation of amount of leaves of forest stand. J. jap. For. Soc. 44: 267-272

Satoo, T. 1967 a. Primary production relations in woodlands of Pinus densiflora. In "Symposium on primary productivity and mineral cycling in natural ecosystems." ed H.E. Young. Univ. Maine Press. pp 52-80

Satoo, T. 1967 b. Efficiency and quantity of leaves of closed stands of Cryptomeria japonica as influenced by site quality. 14th Congr. int. Un. Forest Res. Org. Munich, 1967 Sect. 21: 395-404

Satoo, T. 1968. Primary production and distribution of produced dry matter in a plantation of Cinnamomum camphora. - Materials for the studies of growth in stands. 7. Bull. Tokyo Univ. Forests No 64

Shea, P.F., G.C. Gerloff, and W.H. Gabelman. 1968. Differing efficiencies of potassium utilization in strains of snapbeans, Phaseolus vulgaris L. Pl. Soil 28: 337-346

Shepherd, K.R. 1967. Growth patterns and growth substances in radiata pine. Aust. For. 31: 294-302

Shepherd, K.R. 1968 a. Spacing and thinning in Australian plantations - the future in research. Proc. Silvic. Plantations Working group No 5, Beerwah, 1968

Shepherd, K.R. 1968 b. An experiment with natural regeneration in a radiata pine plantation. Aust. For. 32: 135-142

Shibamoto, T., and T. Tajima. 1961. Leaf analysis of forest trees. 1. The relationship between tree height growth (or soil type) and mineral composition in the needle of Hinoki (Chamaecyparis obtusa Endl.). J. jap. For. Soc. 43: 55-61

Snaydon, R.W. 1962. The growth and competitive ability of contrasting natural populations of Trifolium repens L. on calcareous and acid soils. J. Ecol. 50: 439-447

Snaydon, R.W., and A.D. Bradshaw. 1961. Differential response to calcium within the species Festuca ovina L. New Phytol. 60: 219-234

Snaydon, R.W., and A.D. Bradshaw. 1962. Differences between natural populations of Trifolium repens L. in response to mineral nutrients. I. Phosphate. J. exp. Bot. 13: 422-434

Snedecor, G.W. 1956. Statistical methods. 5th edn. Iowa State Univ. Press, Iowa. 534 pp

Spurr, S.H. 1962. Growth and mortality of a 1925 planting of Pinus radiata on pumice. N.Z. Jl For. 8: 560-569

Steinbeck, K. 1966. Site, height, and mineral nutrient content relations of Scotch pine provenances. Silvae Genet. 15: 42-50

Strickland, R.K., and R.E. Goddard. 1966. Inheritance of branching and crown characteristics in slash pine (Pinus elliottii). Proc. 8th sth. Conf. Forest Tree Improv. Savannah Ga. 1965. pp 57-63

Sweet, G.B. 1964. The effect of physiological age of scion on growth of grafts in Pinus radiata. N.Z. For. Res. Notes 37

Tadaki, Y. 1966. Some discussions on the leaf biomass of forest stands and trees. Bull. Govt. Forest Exp. Stn. Tokyo 184: 135-161

Tamm, C.O. 1955. Studies of forest nutrition. 1. Seasonal variation in the nutrient content of conifer needles. Medd. Skagsform. Inst. Stokh. 45: 1-34

Tukey, H.B., and R.A. Mecklenburg. 1964. Leaching of metabolites from foliage and subsequent reabsorption and redistribution of the leachate in plants. Am. J. Bot. 51: 737-742

Walker, L.C., and R.D. Hatcher. 1965. Variation in the ability of slash pine progeny groups to absorb nutrients. Proc. Soil Sci. Soc. Am. 29: 616-621

Waring, H.D. 1962. Response by Pinus radiata to fertilizer nitrogen and its significance in the maintenance of forest soil fertility. Trans. Int. Congr. Soil Sci. N.Z. 1962

Watson, D.J. 1952. The physiological basis of variation in yield. Advanc. Agron. 4: 101-145

Watson, D.J. 1956. Leaf growth in relation to crop yield. In "The growth of leaves". ed F.L. Milthorpe. Butterworth. London

Weetman, G.F., and R. Harland. 1964. Foliage and wood production in unthinned black spruce in northern Quebec. Forest Sci. 10: 80-88

Wells, C.G., and L.J. Metz. 1963. Variation of nutrient content of loblolly pine needles with season, age, soil and position on the crown. Proc. Soil Sci. Soc. Am. 27: 90-93

White, D.P. 1954. Variation in the nitrogen, phosphorus, and potassium contents of pine needles with season, crown position, and sample treatment. Proc. Soil Sci. Soc. Am. 18: 326-330

White, E.H. 1964. Uptake and distribution of nutrient elements in red pine plantations. Unpub. M.Sc. Thesis Syracuse. New York

Will, G.M. 1957. Variations in the mineral content of radiata pine needles with age and position in the tree crown. N.Z. Jl Sci. Technol. 38B: 699-706

Will, G.M. 1959. Nutrient return in litter and rainfall under some exotic-conifer stands in New Zealand. N.Z. Jl agric. Res. 2: 719-734

Will, G.M. 1961. The mineral nutrient requirements of radiata pine seedlings. N.Z. Jl agric. Res. 4: 309-327

Will, G.M. 1964. Dry matter production and nutrient uptake by Pinus radiata in New Zealand. Commonw. For. Rev. 43: 57-70

Will, G.M. 1966 a. Root growth and dry-matter production in a high-producing stand of Pinus radiata. N.Z. For. Res. Notes 44

Will, G.M. 1966 b. Magnesium deficiency: The cause of spring needle-tip chlorosis in young pines on pumice soils. N.Z. Jl For. 11: 88-94

Will, G.M. 1968. The uptake, cycling and removal of mineral nutrients by crops of Pinus radiata. Proc. N.Z. ecol. Soc. (in press)

Williams, E.J. 1959. Regression analysis. Wiley. New York. 214 pp

Willis, J.B. 1960. The determination of metals in blood serum by atomic absorption spectoscopy. I. Calcium. Spectrochim. Acta 16: 259-272

Willis, J.B. 1963. Analysis of biological materials by atomic absorption spectroscopy. In "Methods of Biochemical Analysis, Vol 11". ed D. Glick. Interscience. New York

Windsor, C.P. 1932. The Gompertz curve as a growth curve. Proc. natn. Acad. Sci. USA 18: 1-8

Witkamp, M., and J. van der Drift. 1961. Breakdown of forest litter in relation to environmental factors. Pl. Soil 15: 295-311

Wood, G.B. 1968. Photosynthesis and growth in Pinus radiata D. Don as affected by environmental factors and inherent qualities. Unpub. Ph.D. Thesis Aust. National Univ. Canberra

Young, H.E., P.N. Carpenter, and R.A. Altenberger. 1965. Preliminary tables of some chemical elements in seven tree species in Maine. Tech. Bull. Maine Agric. Exp. Sta. No 20

Young, H.E., and P.M. Carpenter. 1967. Weight, nutrient element and productivity studies of seedlings and saplings of eight tree species in natural ecosystems. Tech. Bull. Maine Agric. Exp. Sta. No 28

Xydias, G.K. 1964. Dry matter and nutrient-element relations in Pinus resinosa Ait. plantations. Unpub. M.Sc. Thesis Syracuse. New York

Zelawski, W. 1967. Variation in the photosynthetic efficiencies of trees with special reference to Scots pine (Pinus sylvestris L.). Proc. 14th Congr. int. Un. Forest Res. Org. Munich, 1967 Sect. 22: 515-535

APPENDIX 1

Vol.3, No.2 41.

THE ESTIMATION OF OVEN DRY WEIGHT

by W.G. Forrest*

Abstract

Delay before drying, and temperature of drying were examined to determine their effects on oven dry weight estimates for freshly collected P. radiata branchlets. Branchlets lost up to 8% of initial dry weight when stored for extend -ed periods either at room temperature or in a cold room at 7°C, presumably as a result of continued respiration. Branchlets could be stored in the open for 7 days or at 7°C for 17 days before losses exceeded 2% of initial dry weight. Dry weights recorded for branchlets oven dried at 105°C were 2% lower than for branchlets dried at 70°C.

Introduction

Despite the common use of oven dry weight of plant material in biological investigation, few reports are available giving the effects on dry weight values obtained of either the treatment of plant samples prior to oven drying or the temperature at which drying is carried out. Whilst most authors recognise these factors affect oven dry weight estimates, they do not always specify them in presenting results and no standard treatment has gained universal acceptance.

Delay before oven drying is inevitable, particularly where collection sites are distant from laboratories or if oven drying facilities are inadequate. Before plant material is oven dried it may be air dried under varying conditions or stored at low temperatures, but sometimes it receives no special treatment. Evidence that delay in drying might cause serious error has been given by White (1954) who found the nutrient content of Pinus resinosa (Ait.) foliage air-dried for six weeks prior to oven drying was 10% higher than for foliage oven dried immediately after collection due to a decrease in the oven dry weight. In contrast, Humphreys (1958) reported no marked change in the oven dry weights of eucalypt leaves with preliminary air drying for extended periods.

Plant material is usually oven dried within the range 60-105°C. Lower temperatures are used to avoid volatilisation of nitrogen and to lessen the danger of fire; higher temperatures are chosen for rapidity of drying and for conformity with soil analysis for which drying is usually at 105°C.

In this account values are given of changes in oven dry weight estimates resulting -

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(1) from prolonged preliminary storage of green material in -
  (a) a dark, cold room and
  (b) a light, warm laboratory.
(2) from drying at different oven temperatures.

All results are for Pinus radiata (D. Don) branchlets of the 1965-66 growing season, the branchlets being complete individual shoots inclusive of leaves.

Methods

On May 4th, 1966, 50 typical branchlets were collected from the mid-crown position of each of four plantation trees aged 10 years. Branchlets from the four trees were treated separately to give four replications. Three pairs of branchlets from each tree were randomly allocated for each of the following seven pre-drying treatments, the treatments beginning from the time of fresh weight measurements i.e. less than 2 hours from collection.

A oven dried immediately
B air dried in laboratory for 5 days
C air dried in laboratory for 15 days
D air dried in laboratory for 45 days
E held in cold room for 5 days
F held in cold room for 15 days
G held in cold room for 45 days.

In treatments B, C and D the branchlets were kept in an open tray in a light, ventilated laboratory maintained at 16-27°C and 35-60% relative humidity; in treatments E, F and G the branchlets were placed in a dark, unventilated cold room at 7°C and 70-75% relative humidity. After each pre-drying treatment the three branchlet pairs from each tree were re-weighed and oven dried to a constant dry weight in forced-draught ovens. One branchlet pair was dried at 70°C, another at 85°C and the third at 105°C.

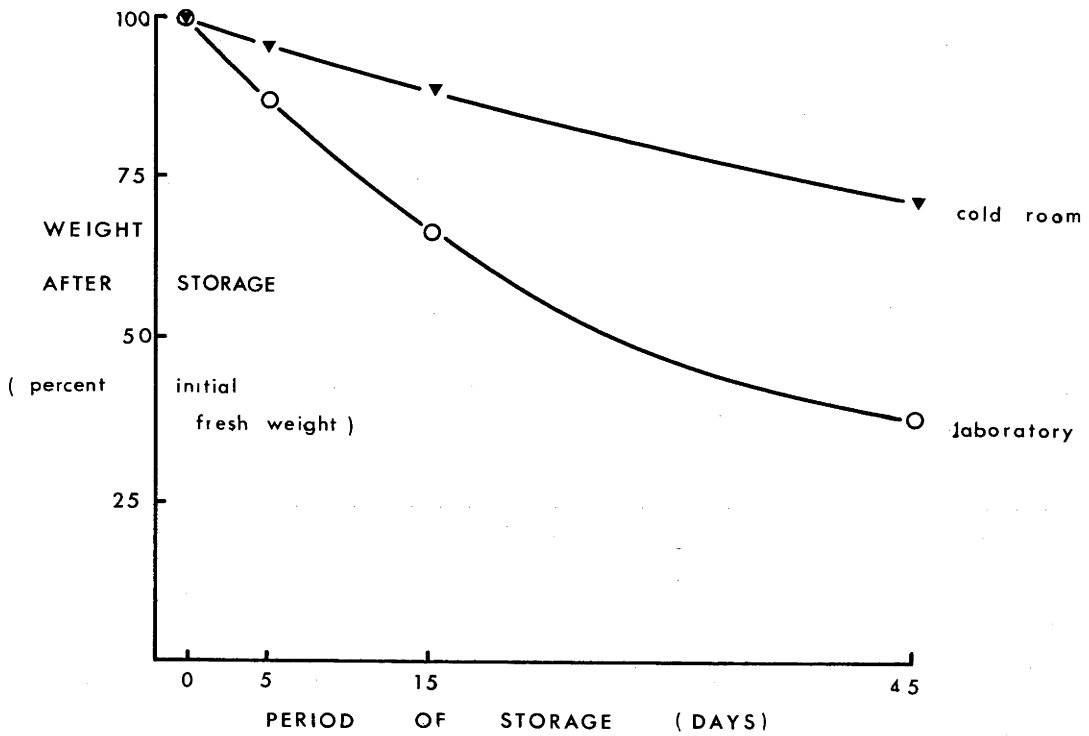
The experiment was designed and analysed statistically as a split-plot experiment with pre-drying storage as the main treatment and temperature of oven-drying as the sub-treatment. Since analysis of variance showed no signifi-cant interaction between treatments and sub-treatments they are discussed inde-pendently.

Results

Storage of branchlets after collection resulted in a loss of weight, the loss becoming progressively greater throughout the 45 day test period (Figure 1). The loss in wet weight of branchlets stored in the cold room was considerably less than for branchlets in the laboratory, the percentage losses being 28.2 and 62.6 respectively after 45 days storage.

In order to see if this weight loss is not simply water loss, the final oven dry weights for each treatment have been calculated and expressed as per-

FIGURE 1. Change in total weight of branchlets held in open laboratory or cold room.



centages of the initial dry weight. The initial dry weights were calculated from initial fresh weights using the average moisture content determined for all branchlets of treatment A, i.e. oven dried immediately after collection.

Analysis of variance of the data summarised in Table 1 shows that the dry weight of branchlets held either in the laboratory or in the cold room progress -ively decreased with time; the loss in weight was statistically significant at 1% level after 15 days in the laboratory or 45 days in the cold room. The progressive change in branchlet weight and composition from an initial 62.5% water and 37.5% dry matter is shown in Fig. 2.

The loss in dry weight of branchlets held in the cold room was initially much less than that of branchlets held in the laboratory. After 45 days branchlets stored in laboratory and cold room had lost 2.9 and 2.5% respectively of the initial fresh weight. These losses are equivalent to 7.8% and 6.7% respectively of the oven dry weight of branchlets dried immediately after collection (treatment A) and thus indicate the error likely to occur in dry weight estimation with such storage

The slight increase in dry weight of branchlets stored for 5 days in the

cold room was examined in more detail. No similar increase in weight was obtained in the repeat experiment and the dry weight increase in treatment E probably results from natural variation in the material used (as indicated also by the analysis of variance).

The effects of temperature during oven drying are less marked than those of pre-drying treatment. The weights for branchlets dried at 70, 85 and 105°C, averaged for all storage treatments are 97.9, 97.1 and 95.8% of initial dry weight respectively, the first differing significantly from the last at the 1% level. Thus drying at 105°C has given an estimate of oven dry weight 1.3% lower than drying at 85°C and 2.1% lower than drying at 70°C.

TABLE 1. Oven dry weights as percentage of calculated initial dry weight (Means of 4 replicates)

	Storage	Temperature of Oven Drying 70°C	85°C	105°C	Mean
A	NIL	101.04	100.80	98.48	100.09
B	Laboratory - 5 days	99.47	98 69	97.49	98.55
C	Laboratory - 15 days	95.59	94.98	94.41	94.99
D	Laboratory - 45 days	93.40	92.40	91.28	92.36
E	Cold Room - 5 days	101.44	100.86	99.39	100.56
F	Cold Room - 15 days	99.27	99 04	97.14	98.48
G	Cold Room - 45 days	95.04	93.01	92.48	93.51
	Mean	97.89	97.11	95.81	96.94

Analysis of variance shows significant differences at 1% level between means for both storage treatments and temperature subtreatments.

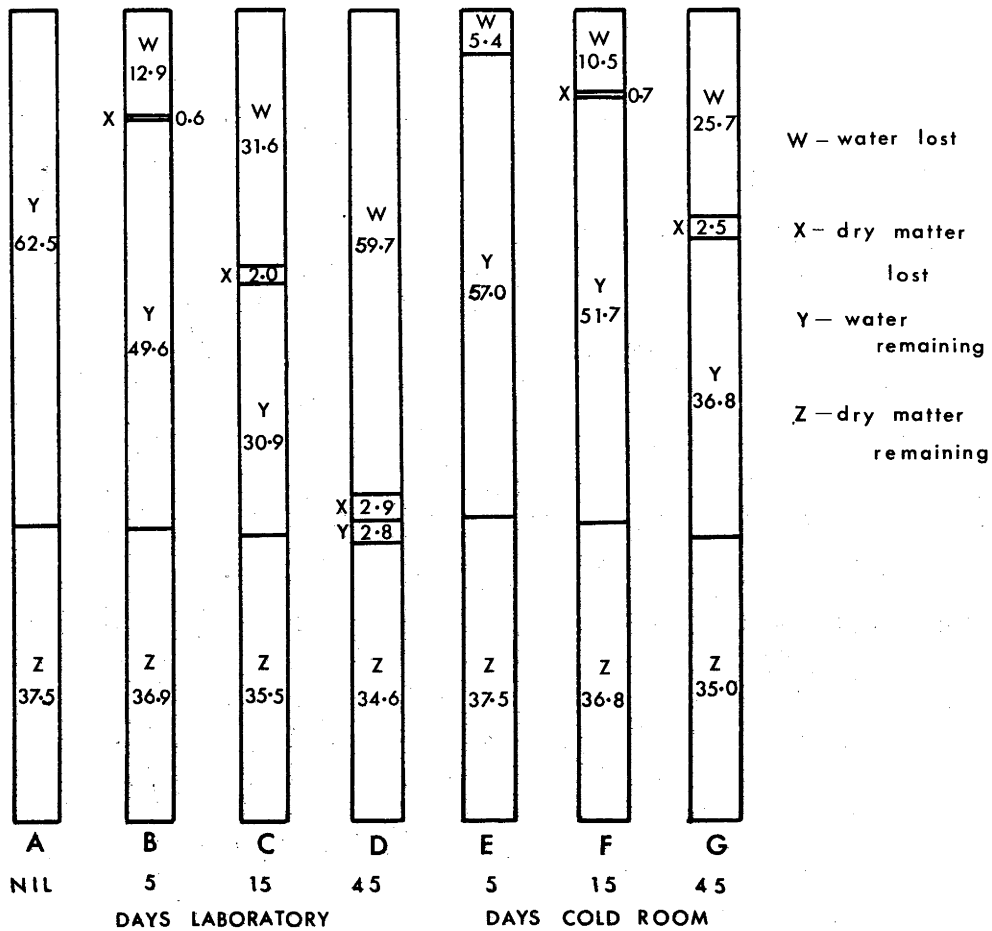
Least difference for significance between storage treatment means = 3.77 (1%)

Least difference for significance between drying temperature subtreatment means = 1.63 (1%)

Discussion

Investigations of organic production, energy flow and nutrient circulation involve extensive outdoor sampling and later determination of fresh and dry

FIGURE 2. Progressive change in branchlet weight and composition with storage.



weights. Significant errors may be introduced into such investigations, depending on the treatment of plant material after sampling.

After cutting, the weights of green branchlets of P. radiata rapidly decreased so that after 45 days in the laboratory and cold room the branchlets were about 60% and 30% respectively of their initial fresh weight. These weight changes can be attributed to various causes including water loss, decomposition, respiration and photosynthesis. Water loss is of greatest importance and may account for 90%-100% of the total weight loss from fresh to oven dry depending on the type and duration of storage.

Weight changes attributable to factors other than moisture loss, although much smaller than those caused by water loss, are important because they are changes also to the oven dry weight. Some photo-synthesis may have

occurred in branchlets after collection but if so the resultant increase in weight was small in comparison with the overall decrease. Since there was no evidence of micro-bial activity, the decrease in branchlet dry weight with storage probably resulted primarily from respiration.

The low temperature of the cold room apparently reduced the rate of respiration considerably such that no loss in dry weight was evident after one week of storage, but after an extended period branchlets lost approximately 8% of dry matter both in the open laboratory and in the cold room. Delay in oven drying plant material will result in a serious underestimate of oven dry weight, increasing with length of storage even at low temperatures. Drying should be completed, at least to equilibrium moisture content, as quickly as possible.

Increasing the temperature at which oven drying is carried out slightly decreases the constant oven dry weight of pine branchlets. Raising the oven temperature from 70° to 105°C lowered the dry weight by 2%. Drying plant material at over 100°C increases the risk of fire and of organic volatilisation. For most purposes standardisation of oven drying at 85°C would seem acceptable.

References

Humphreys, F.R. (1958) - The occurrence of rutin in the extraction of rutin from the foliage of commercially important N.S.W. species. Div. Wood Tech. For. Comm. N.S.W. Project C.12 Final Report.

White, D.F. (1954) - Variation in the nitrogen, phosphorus and potassium contents of pine needles with season, crown position and sample treatment. Soil Sci. Soc. Amer. Proc. 18: 326-330.

APPENDIX 2 Size dimensions of trees in *P. radiata* 100-tree study plot, Stromlo Plantation

Tree number	Bole diameter (cm) at 130 cm	crown	ground	Tree height (m)	Average crown depth (m)	crown diameter (m)
1	11.8	14.7	15.3	6.22	5.79	3.32
2	16.1	20.3	21.0	7.19	6.92	4.51
3	12.6	15.4	16.8	8.05	7.65	3.63
4	8.7	10.4	8.9	5.97	5.36	2.01
5	12.8	16.0	17.5	7.65	7.10	3.81
6	12.3	20.0	15.4	9.24	8.96	3.35
7	15.8	18.6	21.6	10.12	9.48	3.66
8	10.9	14.0	14.8	7.92	7.59	3.32
9	11.9	14.3	16.6	8.78	8.35	2.74
10	12.2	14.3	15.1	5.97	5.46	3.69
11	12.2	13.7	14.6	7.68	7.04	2.87
12	14.9	17.5	19.8	8.84	7.89	4.08
13	16.1	20.1	20.7	7.65	7.38	4.21
14	16.4	23.6	24.6	6.00	5.73	4.18
15	13.3	16.8	17.8	7.96	7.65	3.23
16	16.2	18.8	19.2	9.85	9.57	3.60
17	13.5	15.0	16.9	9.36	8.69	3.41
18	11.3	16.1	16.6	7.62	7.38	3.35
19	6.5	7.7	8.3	4.72	4.21	1.55
20	3.9	5.1	5.8	4.63	4.21	1.22
21	14.3	17.7	17.8	8.81	8.56	3.41
22	12.5	13.6	15.7	7.80	7.44	3.57
23	14.4	19.6	20.1	9.42	9.34	3.41
24	16.8	16.5	19.8	9.52	9.24	3.29
25	11.1	13.0	15.2	6.92	6.10	2.99
26	14.7	18.9	19.3	9.51	9.27	3.90
27	11.7	14.1	15.0	7.07	6.71	3.72
28	5.1	6.6	6.6	4.94	4.79	1.49
29	17.6	21.1	21.6	9.81	9.48	4.72
30	12.5	15.5	15.6	7.89	7.71	3.87
31	14.0	16.4	18.1	7.10	6.46	3.51
32	9.0	11.6	12.7	6.64	5.88	2.22
33	13.8	17.8	19.3	8.78	8.38	3.72
34	15.3	17.9	21.4	9.94	9.08	3.41
35	12.5	15.9	16.2	7.50	7.25	3.72
36	12.4	15.1	16.0	8.75	8.50	3.44
37	13.3	16.5	17.3	9.54	9.24	3.26
38	15.3	18.9	19.4	9.54	9.30	4.82
39	5.3	5.0	6.1	5.43	3.99	4.11
40	7.4	9.5	10.4	6.28	5.88	2.68
41	15.7	17.8	21.4	9.14	8.14	4.11
42	11.0	12.5	21.9	7.56	6.68	2.68
43	15.3	17.5	19.1	9.66	8.90	3.23
44	16.4	19.2	19.4	8.75	8.41	4.36

APPENDIX 2 (continued) Size dimensions of trees in *P. radiata* 100-tree study plot, Stromlo Plantation

Tree number	Bole diameter (cm) at 130 cm	crown	ground	Tree height (m)	Average crown depth (m)	crown diameter (m)
45	14.2	16.7	17.9	7.68	7.19	3.72
46	12.0	14.5	14.6	4.97	4.72	2.16
47	16.5	21.3	22.4	8.17	7.92	4.11
48	10.4	12.4	14.0	7.19	6.71	2.74
49	13.9	15.9	17.0	8.53	8.02	3.51
50	15.0	16.8	18.9	9.36	8.75	3.17
51	10.6	12.8	14.0	8.47	7.86	2.68
52	16.7	20.6	22.2	8.75	8.53	4.15
53	11.7	16.0	15.9	8.47	8.32	3.08
54	12.0	13.7	14.5	7.38	6.68	3.23
55	16.7	20.3	20.6	9.51	9.20	3.54
56	15.1	17.6	19.8	8.96	8.44	3.11
57	21.5	21.5	20.9	9.05	8.93	3.26
58	13.4	16.5	17.2	8.32	8.11	3.35
59	6.2	7.2	7.2	5.33	5.24	1.43
60	12.9	16.4	16.8	7.32	7.07	3.02
61	10.7	13.2	13.2	6.00	5.85	2.90
62	14.7	18.8	18.9	9.14	8.99	4.39
63	16.0	20.3	20.6	7.38	7.07	4.02
64	14.6	16.9	18.6	8.26	7.68	3.05
65	10.6	13.3	14.6	8.78	8.50	4.08
66	13.7	17.6	17.4	8.99	8.84	3.66
67	14.4	17.7	18.9	10.00	9.51	4.63
68	15.5	19.6	19.9	9.48	9.27	4.21
69	13.8	17.4	18.0	10.18	9.91	3.41
70	9.7	11.2	12.4	6.64	6.40	2.80
71	5.6	8.1	7.9	4.79	4.66	1.25
72	10.9	14.2	15.1	6.46	6.13	2.96
73	16.4	21.9	21.8	9.57	9.39	3.78
74	14.9	19.9	21.0	9.75	9.45	5.49
75	14.2	18.7	19.7	8.38	8.08	3.84
76	12.0	13.6	14.3	7.86	7.19	2.93
77	14.1	18.7	18.8	9.57	9.36	4.69
78	14.0	16.9	17.6	9.30	8.90	3.32
79	15.5	19.1	22.1	5.73	5.21	4.27
80	13.3	15.1	16.5	8.23	7.38	3.96
81	8.0	8.7	11.5	5.85	5.27	2.80
82	14.0	16.3	17.4	9.08	8.63	3.87
83	14.0	17.4	18.3	9.05	8.78	3.05
84	7.8	8.8	9.7	6.95	6.37	3.84
85	9.0	11.2	11.4	6.95	6.83	2.68
86	13.1	16.9	17.7	8.08	7.77	3.14
87	12.7	15.0	13.6	8.81	8.26	2.68

APPENDIX 2 (continued) Size dimensions of trees in *P. radiata* 100-tree study plot, Stromlo Plantation

Tree number	Bole diameter (cm) at 130 cm	crown	ground	Tree height (m)	Average crown depth (m)	crown diameter (m)
88	12.4	14.5	15.0	8.32	7.89	3.32
89	12.0	16.5	17.1	7.04	6.77	3.72
90	13.4	16.1	17.8	9.39	8.81	3.38
91	12.3	14.5	15.4	7.92	7.38	2.68
92	13.2	18.5	18.7	8.90	8.87	3.05
93	15.1	18.2	18.8	9.08	8.84	3.51
94	16.0	19.8	20.0	9.75	9.57	4.05
95	12.6	15.7	15.6	7.99	7.71	2.93
96	14.4	20.9	20.3	8.08	7.96	4.42
97	14.5	15.5	19.3	8.72	7.77	2.96
98	15.2	18.8	20.3	9.81	9.48	4.02
99	13.8	16.0	17.8	7.86	7.28	3.17
100	10.8	16.0	14.7	2.68	2.50	2.80

APPENDIX 3 Dry weight of trees in P. radiata study plot, Stromlo Plantation

Tree number	Dry weights (kg) Boles	Live branches	Leaves	Roots	Dead branches	Male cones	Female cones	Total weight
1	12.70	10.99	7.03	6.18	1.27	0.07	0	38.23
2	32.79	28.95	14.99	12.70	0.42	0.84	0.07	90.76
3	19.29	13.54	7.96	8.19	0.58	0.58	0.33	50.46
4	5.84	5.10	1.76	1.72	1.66	0.03	0	16.11
5	17.80	16.44	7.72	8.34	0.34	0.15	0	50.80
6	21.93	12.27	8.74	10.50	0.32	0.22	0.01	53.97
7	30.33	21.44	10.82	15.95	1.75	0.24	0	80.54
8	17.03	9.24	5.27	5.00	0.61	0.71	1.28	39.14
9	16.28	5.80	6.50	6.13	0.38	0.14	0.02	35.25
10	18.02	9.16	7.00	6.08	0.23	0.50	0	40.98
11	15.15	8.67	6.56	4.61	1.02	0.39	0	36.40
12	31.50	17.22	7.87	11.91	2.42	0.63	0.38	71.93
13	29.12	25.47	14.86	12.09	0.25	0.51	0	82.29
14	28.47	24.07	13.83	19.26	1.06	0.85	0	87.54
15	21.08	15.15	9.13	8.39	0.34	0.16	0	54.24
16	33.87	17.73	12.17	13.82	1.00	0.31	0.01	78.91
17	25.43	11.63	6.20	6.79	2.19	0.36	0	52.60
18	14.25	13.92	4.27	7.02	0.99	0.30	0	40.75
19	3.09	1.64	0.33	1.65	0.48	0.03	0	7.23
20	0.85	0.68	0.38	1.00	0.13	0.03	0	3.07
21	24.38	9.45	11.93	11.57	0.27	0.11	0.21	57.92
22	24.52	8.36	4.61	7.27	1.09	0.32	0.55	46.72
23	25.93	14.33	7.97	8.55	0.63	0.15	0.03	57.59
24	34.95	26.92	15.05	11.19	3.31	0.20	0.01	91.62
25	13.81	6.05	3.44	4.79	2.18	0.15	0	30.41
26	30.11	18.16	11.82	10.47	2.13	0.11	2.88	75.67
27	20.97	5.91	3.81	6.21	0.43	0.30	0.50	38.12
28	2.05	1.01	0.91	0.55	0.01	0.03	0	4.56
29	37.26	34.33	18.88	15.82	0.96	0.81	0	108.06
30	20.83	11.16	6.62	6.13	2.47	0.03	0	47.24
31	21.66	20.48	8.30	7.26	2.15	0.42	0	60.26
32	10.01	5.67	2.81	2.86	3.31	0.18	0	24.85
33	25.25	13.81	8.59	9.64	1.37	0.55	0.01	59.22
34	33.55	17.11	11.99	12.96	1.16	0.32	0	77.09
35	15.86	10.06	6.72	5.92	0	0.28	0	38.84
36	19.73	6.46	6.35	8.86	0.69	0.19	0.21	42.48
37	25.38	10.59	9.19	9.42	0.47	0.01	0	55.06
38	30.40	18.43	11.93	12.27	0.22	0.42	0.11	73.77
39	2.12	0.39	0.61	0.45	0.10	0.03	0	3.69
40	5.27	1.40	1.69	1.42	0.13	0.06	0	9.97
41	31.05	18.75	12.41	9.90	2.00	0.58	0.46	75.15
42	14.25	6.71	3.71	3.59	2.66	0.09	0.18	31.19
43	32.44	15.16	9.51	12.21	0.94	0.09	0.15	70.50

APPENDIX 3 (continued) Dry weight of trees in *P. radiata* study plot, Stromlo Plantation

Tree number	Dry weights (kg) Boles	Live branches	Leaves	Roots	Dead Branches	Male cones	Female cones	Total weight
44	29.86	20.82	11.21	11.27	1.30	0.57	0.13	75.15
45	21.82	16.23	8.21	11.49	0.42	0.15	0	58.33
46	13.23	7.24	4.66	3.75	1.08	0.05	0	30.00
47	27.09	26.12	15.13	13.59	0.69	1.42	0.03	84.05
48	13.62	4.37	5.22	4.87	0.54	0.13	0	28.74
49	26.51	12.00	10.54	7.37	1.52	0.26	0.06	58.25
50	24.17	11.92	8.77	10.07	1.03	0.07	0	56.02
51	15.44	8.10	4.68	4.13	0.87	0.07	0.18	33.48
52	31.35	27.82	13.06	17.27	1.19	0.25	0	90.93
53	18.81	6.15	4.51	6.09	0.01	0.13	0	35.69
54	16.15	10.55	7.80	6.10	2.32	0.43	0.10	43.46
55	32.87	27.90	18.03	10.58	0.50	0.80	0.13	90.81
56	25.64	19.41	12.73	10.07	1.56	0.03	0.01	69.44
57	43.94	50.66	28.80	24.13	1.69	0.30	0.05	149.57
58	19.96	16.33	7.81	8.83	0.13	0.17	0	53.23
59	3.22	1.26	1.32	1.12	0.02	0.03	0	6.98
60	19.34	11.18	8.98	7.00	0.10	0.35	0	46.95
61	8.77	7.84	4.09	4.86	0.05	0.08	0	25.69
62	26.60	17.82	13.72	13.47	0.24	0.07	1.32	73.26
63	26.19	21.38	11.63	14.92	1.80	0.08	0.01	76.00
64	25.85	14.31	8.54	9.04	0.87	0.05	0	58.66
65	16.16	6.46	6.20	3.95	0.36	0.04	0.43	33.60
66	23.81	16.82	8.31	10.00	0.49	0.10	0.02	59.55
67	29.05	22.44	12.51	13.32	0.90	0.14	0.01	78.36
68	31.74	25.35	15.15	13.78	1.02	0.15	0	87.18
69	29.35	11.45	11.42	8.73	0.12	0.03	0.12	61.22
70	10.71	4.75	4.12	3.43	0.11	0	0.12	23.24
71	2.58	0.77	1.08	0.72	0.04	0	0	5.20
72	12.90	8.84	5.73	4.22	0.04	0.07	0	31.80
73	39.00	17.69	13.42	17.67	0.92	0.05	0.10	88.85
74	32.98	24.12	12.68	14.17	0.07	0.05	0	84.07
75	24.85	17.50	9.89	11.87	0.02	0.23	0	64.37
76	18.88	5.04	3.67	5.06	0.76	0.02	0	33.42
77	21.21	16.04	11.51	11.26	0.02	0	0.91	60.95
78	28.07	13.74	9.30	8.31	0.21	0.08	0.35	60.06
79	33.51	23.28	15.25	10.06	0.57	0.22	0	82.90
80	23.19	15.32	9.66	8.71	1.53	0.15	0	58.56
81	5.25	3.57	2.56	2.06	0.98	0.14	0	14.85
82	23.43	13.41	7.92	10.62	0.63	0.15	0.18	56.33
83	25.61	12.41	11.15	9.31	0.21	0.19	0.59	59.46
84	5.98	2.19	2.12	2.19	0.20	0.07	0	12.76
85	8.14	5.07	2.99	2.54	0.09	0.02	0	18.85
86	22.91	13.52	8.36	9.06	0.13	0.14	0.26	54.37
87	20.18	8.16	6.72	5.82	0.56	0.16	0	41.59

APPENDIX 3 (continued) Dry weight of trees in P. radiata study plot, Stromlo Plantation

Tree number	Dry weights (kg) Boles	Live branches	Leaves	Roots	Dead Branches	Male cones	Female cones	Total weight
88	16.58	9.28	7.34	6.41	0.35	0.11	0.11	40.09
89	19.99	12.61	6.96	6.79	0.32	0.13	0.03	46.83
90	25.79	10.22	9.27	9.06	0.92	0.26	0	55.52
91	19.70	7.63	6.39	5.35	1.08	0.22	0	40.36
92	21.00	11.08	9.40	6.95	0.19	0.37	0	48.98
93	27.87	21.41	9.55	10.81	0.02	0.25	0.03	69.93
94	34.78	20.62	12.67	15.53	0.82	0.06	0	84.47
95	18.69	9.99	6.11	8.48	0.34	0.12	0	43.73
96	24.57	20.72	10.40	11.23	0	0.61	0	67.52
97	28.93	13.75	8.15	12.53	0.76	0.04	0	64.16
98	33.97	21.92	13.88	16.08	1.44	0.07	0.40	87.75
99	25.15	14.02	8.53	8.75	2.12	0.04	0.01	58.61
100	8.42	12.64	4.11	4.24	1.81	0.07	0	31.29

APPENDIX 4 P. radiata clone study size class frequency distribution. Numbers of stems per bole diameter class

Diameter class (cm)	1961 Clone Block							1962 Clone Block		
	546 A	579 A	582 A	602 A	605 A	954	Total **	546 A	602 A	605 A
1.90- 2.54									1	
2.55- 3.18						3	35	2	1	
3.19- 3.81	1	1	2	2		5	135	4	5	2
3.82- 4.45		1	4	1		2	100		3	2
4.46- 5.09	4	1	2	4		1	160	1	3	
5.10- 5.72	1	4	5	3	1	4	235	3		2
5.73- 6.35	3	2	3		4	3	200	4		2
6.36- 6.99	3	7	2	2	1	1	200	3	3	
7.00- 7.62	2		2		3	1	110	1	3	
7.63- 8.26	4	2		2	2		124		1	1
8.27- 8.89	1	1		3	3		110	1		1
8.90- 9.53		1			1		25	1		1
9.54-10.16	1						12			1
10.17-10.80					2		25			
10.81-11.43					1		12			
Total	20	20	20	17	18	20	1483	20	20	12

** Total column indicates stocking density per hectare overall in 1961 Clone block.

APPENDIX 5

Number of branches per tree in
P. radiata clone study

Tree number	Clone 546A	579A	582A	602A	605A	954
1	77	69	50	37	61	56
2	61	54	49	49	74	69
3	76	46	53	52	66	54
4	56	54	52	55	64	60
5	76	62	46	30	63	50
6	62	67	61	43	62	62
7	61	61	51	35	55	42
8	73	53	42	28	52	51
9	44	59	54	27	58	50
10	30	42	34	36	66	32
11	46	66	49	48	49	27
12	43	41	35	37	65	39
13	41	40	37	33	52	74
14	59	60	25	26	53	34
15	43	69	38	28	54	46
16	58	64	50	38	57	32
17	41	53	35	28	48	50
18	31	34	47		42	61
19	40	34	41			45
20	61	64	34			39
Mean	53.95	54.60	44.15	37.06	57.83	48.65

APPENDIX 6

Number of whorls per tree in
P. radiata clone study

Tree number	Clone 546A	579A	582A	602A	605A	954
1	16	13	11	7	10	11
2	13	10	13	11	13	13
3	17	9	12	11	10	12
4	14	10	12	11	12	13
5	15	11	12	5	11	12
6	14	13	10	8	12	11
7	14	10	11	8	11	10
8	16	10	9	5	10	11
9	11	11	12	8	12	11
10	8	7	9	7	12	8
11	12	11	11	8	10	7
12	9	9	7	8	13	9
13	11	9	8	6	9	14
14	13	11	6	6	10	7
15	9	13	9	5	9	11
16	15	13	11	6	11	7
17	9	9	8	5	11	11
18	9	8	10		9	11
19	10	6	8			10
20	13	13	8			10
Mean	12.40	10.30	9.85	7.35	10.83	10.45

APPENDIX 7

Average branch diameter in trees of *P. radiata* clone study (mm)

Tree number	Clone 546A	579A	582A	602A	605A	954
1	11.25	11.97	13.60	14.00	18.16	9.21
2	8.92	10.65	9.35	13.31	11.72	9.26
3	10.95	13.13	11.81	13.88	14.68	8.63
4	10.39	11.91	10.35	13.45	11.17	9.18
5	12.93	10.95	9.91	11.97	14.32	8.00
6	10.68	12.00	11.49	12.91	12.31	7.66
7	12.79	10.51	11.96	13.17	12.87	7.19
8	11.55	11.74	9.45	12.18	12.44	9.57
9	10.48	9.75	10.20	7.67	13.60	7.42
10	11.23	12.24	12,88	14.14	13.71	6.44
11	9.17	10.08	10.57	15.35	10.94	5.96
12	10.74	9.49	10.03	10.16	16.29	7.10
13	10.24	11.13	8.05	10.39	13.10	8.57
14	11.19	13.48	8.40	11.46	10.34	5.68
15	11.58	12.66	9.73	10.25	10.06	6.57
16	9.93	9.48	8.66	12.00	10.21	7.16
17	9.63	10.19	11.49	13.07	11.50	8.66
18	8.06	9.68	8.87		11.10	7.41
19	9.20	8.38	10.97			6.51
20	11.54	9.91	11.03			6.82
Mean	10.62	10.97	10.44	12.31	12.70	7.65

APPENDIX 8 a

P. radiata Clone Study Clone 546 A
Summary of size and weight of sample branches

Tree Number	Whorl Number	Branch Diameter (mm)	Dry weight (gm) Wood	Leaves	Total
1	5	12	15.02	41.27	56.29
1	8	15	43.92	81.28	125.20
2	3	7	4.51	11.86	16.37
2	7	18	86.59	154.24	240.83
3	6	12	16.40	42.32	58.72
3	15	20	132.48	173.24	305.72
4	5	12	23.58	44.75	68.33
4	9	7	5.76	23.12	28.88
5	10	19	103.53	174.86	278.39
5	14	17	100.48	156.06	256.54
6	4	11	14.56	33.55	48.11
6	10	16	54.62	107.86	162.48
7	7	17	77.76	106.70	184.46
7	9	16	61.83	114.63	176.46
8	11	13	38.64	87.93	126.57
8	15	19	129.43	198.47	327.90
9	2	6	2.00	6.40	8.40
9	11	14	50.46	74.93	125.39
10	5	14	50.80	95.12	145.92
10	6	15	65.48	90.73	156.21
11	3	10	12.52	26.57	39.09
11	8	11	26.26	69.83	96.09
12	1	9	10.36	14.04	24.40
12	5	14	53.81	101.67	155.48
13	4	10	12.14	27.58	39.72
13	10	18	105.58	175.12	280.70
14	6	9	10.93	35.12	46.05
14	13	11	31.43	40.84	72.27
15	2	7	4.40	11.10	15.50
15	8	21	141.10	169.08	310.18
16	7	12	21.88	50.84	72.72
16	14	15	50.88	86.44	137.32
17	3	7	4.80	18.79	23.59
17	8	15	49.00	80.59	129.59
18	1	5	1.39	4.91	6.30
18	6	7	6.30	23.96	30.26
19	4	11	16.92	44.30	61.22
19	10	16	65.76	92.44	158.20
20	9	16	45.90	98.72	144.62
20	12	18	78.50	132.56	210.76

APPENDIX 8 b

P. radiata clone study Clone 579 A
Summary of size and weight of sample branches

Tree Number	Whorl Number	Branch Diameter (mm)	Dry weight (gm) Wood	Leaves	Total
1	3	14	18.36	43.70	62.06
1	6	13	38.93	98.06	136.99
2	4	11	20.01	50.96	70.97
2	8	14	51.81	62.86	114.67
3	2	12	28.86	23.73	52.59
3	5	5	2.96	9.36	12.32
3	8	34	496.15	443.48	939.63
4	6	19	129.28	231.15	360.43
4	9	24	236.41	248.76	485.17
5	5	10	18.73	46.50	65.23
5	8	11	26.63	68.98	95.61
6	2	11	21.98	19.62	41.60
6	7	6	2.60	13.53	16.13
7	7	12	32.72	65.42	98.14
7	10	17	100.74	128.87	229.61
8	1	10	8.13	5.37	13.50
8	8	18	96.92	137.88	234.80
9	3	11	14.90	24.01	38.91
9	9	14	41.21	93.69	134.90
10	1	7	5.03	7.46	12.49
10	4	11	23.52	64.14	87.66
11	5	15	46.44	81.41	127.85
11	9	18	105.51	153.83	259.34
12	1	8	3.50	3.84	7.34
12	6	13	33.80	77.33	111.13
13	3	13	37.82	64.75	102.57
13	6	15	54.33	104.62	158.95
14	7	16	74.96	133.65	208.61
14	11	18	133.73	201.85	335.58
15	3	9	7.70	22.69	30.39
15	8	13	43.38	94.09	137.47
16	2	11	14.95	24.14	39.09
16	5	8	8.40	32.49	34.89
17	2	13	24.95	46.11	60.25
17	6	11	18.10	49.59	67.69
18	4	15	51.33	90.34	141.67
18	6	8	8.94	29.98	39.12
19	3	9	10.05	29.74	39.79
19	5	14	40.15	86.43	126.58
20	6	11	18.65	49.31	67.96
20	9	12	23.68	61.71	85.39

APPENDIX 8 c

P. radiata clone study Clone 582 A
Summary of size and weight of sample branches

Tree Number	Whorl Number	Branch Diameter (mm)	Branch dry weight (gm) Wood	Leaves	Total
1	3	13	35.56	63.01	98.57
1	6	19	102.13	129.72	231.85
2	8	9	12.89	40.65	53.54
2	11	9	12.19	24.07	36.26
3	4	14	31.52	61.64	93.16
3	6	12	22.49	54.91	77.40
3	10	14	38.31	70.26	108.57
3	10(2)	17	79.24	122.98	202.22
4	4	9	7.09	20.72	27.81
4	7	12	20.03	52.39	72.42
5	2	6	2.82	7.68	10.50
5	5	12	18.13	46.49	64.62
7	4	7	5.52	16.17	21.69
7	8	13	27.01	77.45	104.46
8	1	7	4.71	8.45	13.16
8	5	10	16.44	32.44	44.88
9	9	13	37.12	66.69	103.81
9	11	10	19.99	38.66	58.65
10	3	7	4.54	15.01	19.55
10	7	14	56.89	81.71	138.60
11	3	5	1.58	7.42	9.00
11	10	12	28.41	52.60	81.01
12	2	8	6.98	15.59	22.57
12	6	7	5.76	12.00	17.76
13	5	9	10.37	26.47	36.84
13	7	10	15.94	35.35	51.29
14	1	4	0.93	4.21	5.14
14	6	9	14.53	18.48	33.01
15	3	7	4.28	14.31	18.59
15	7	16	50.38	91.29	141.67
16	4	8	9.58	24.54	34.12
16	9	8	7.38	18.55	25.93
17	2	11	17.74	30.63	48.37
17	8	17	79.42	70.50	149.92
18	3	8	5.20	14.90	20.10
18	9	13	27.95	50.10	78.05
19	5	15	36.64	65.60	102.24
19	7	16	47.01	86.71	133.72
20	4	12	22.17	48.35	70.52
20	8	21	81.44	136.74	218.18

APPENDIX 8 d

P. radiata clone study Clone 602 A
Summary of size and weight of sample branches

Tree Number	Whorl Number	Branch Diameter (mm)	Branch dry weight (gm) Wood	Leaves	Total
1	2	20	96.28	108.44	204.72
1	7	11	35.12	67.78	102.90
2	5	12	29.90	63.56	93.46
2	8	12	31.42	64.66	96.08
3	3	20	88.60	87.96	176.56
3	10	13	51.02	96.86	147.88
4	3	16	38.72	57.94	96.66
4	7	22	204.98	257.94	462.92
5	2	14	41.10	67.78	108.88
5	5	6	4.00	13.66	17.66
6	4	16	60.06	92.50	152.56
6	7	21	161.34	234.10	395.44
7	5	19	126.83	161.05	287.88
7	8	17	117.88	146.24	264.12
8	2	12	24.89	50.97	75.86
8	3	16	75.10	126.19	201.29
9	1	7	4.20	12.40	16.60
9	7	12	33.01	48.57	81.58
10	3	15	66.21	101.00	167.21
10	6	17	74.48	111.86	186.34
11	2	18	66.32	68.90	135.22
11	8	6	3.96	9.15	13.11
12	1	6	1.71	6.00	7.71
12	6	17	88.61	134.36	222.97
13	1	10	10.88	23.38	34.26
13	2	12	25.55	51.69	77.24
14	1	11	13.70	27.22	40.92
14	3	17	73.33	116.87	190.20
15	2	13	22.26	34.66	56.92
15	4	18	77.18	139.52	216.70
16	2	15	39.93	68.30	108.23
16	5	10	16.98	43.82	60.80
17	3	19	101.49	158.51	260.00
17	4	13	47.34	88.21	135.55

APPENDIX 8 e

P. radiata clone study Clone 605 A
Summary of size and weight of sample branches

Tree Number	Whorl Number	Branch Diameter (mm)	Branch dry weight (gm) Wood	Leaves	Total
1	5	24	219.18	225.81	444.99
1	8	32	394.90	467.34	862.24
2	5	14	37.30	76.42	113.72
2	9	11	19.19	50.46	69.65
3	3	16	63.62	96.96	160.58
3	7	18	98.53	172.64	271.17
4	2	10	9.90	18.88	28.78
4	10	17	70.02	127.35	197.37
5	2	11	12.02	20.88	32.90
5	8	18	86.72	161.70	248.42
6	5	14	48.16	108.68	156.84
6	7	15	46.24	82.98	129.22
7	1	13	31.64	28.98	60.62
7	9	23	156.49	241.75	398.24
8	4	12	34.88	45.39	70.27
8	7	23	153.89	219.21	373.10
9	3	9	5.74	23.02	28.76
9	7	16	61.62	116.70	178.32
10	8	16	75.93	108.89	184.82
10	11	23	214.30	285.36	499.66
11	6	12	26.74	66.67	93.41
11	8	20	123.86	205.38	329.24
12	3	21	122.28	122.32	244.60
12	12	12	45.24	91.70	136.94
13	4	12	25.38	52.68	78.06
13	9	16	72.88	135.22	208.10
14	2	8	7.34	8.38	15.72
14	6	15	53.04	81.48	134.52
15	6	15	47.62	92.14	139.76
15	8	19	92.90	149.50	242.40
16	5	10	14.56	35.08	49.64
16	7	14	37.32	83.59	120.91
17	3	11	10.18	23.82	34.00
17	9	22	123.44	190.58	314.02
18	1	10	8.08	16.98	25.06
18	6	13	27.56	63.62	91.18

APPENDIX 8 f

P. radiata clone study Clone 954
Summary of size and weights of sample branches

Tree Number	Whorl Number	Branch Diameter (mm)	Branch dry weights (gm) Wood	Leaves	Total
1	3	9	8.04	25.53	33.57
1	7	12	29.18	87.28	116.46
2	6	13	26.07	80.43	106.50
2	12	9	18.47	27.93	46.40
3	2	11	18.77	31.86	50.63
3	5	10	15.53	50.46	65.99
4	4	9	7.04	25.18	32.22
4	12	9	10.54	27.82	38.36
5	7	10	12.44	40.39	52.83
5	11	13	41.65	108.65	150.30
6	3	6	2.51	10.47	12.98
6	10	8	7.19	22.89	30.08
7	2	10	9.08	19.15	28.23
7	6	8	6.73	29.60	36.33
8	5	11	20.77	63.40	84.17
8	11	12	34.58	88.84	123.42
9	2	7	5.34	14.60	19.94
9	10	13	28.96	94.60	123.56
10	1	8	4.48	7.38	11.86
10	5	5	1.46	9.02	10.48
11	3	7	4.54	14.15	18.69
11	7	9	7.01	30.84	37.85
12	4	3	0.18	0.96	1.14
12	7	8	6.31	26.93	33.24
13	5	11	19.98	57.81	77.79
13	12	10	16.54	39.22	55.76
14	1	5	1.93	6.43	8.36
14	6	8	7.80	33.24	41.04
15	3	7	5.10	18.27	23.37
15	11	6	3.22	4.18	7.40
16	4	7	5.35	24.58	29.93
16	5	9	7.45	37.38	44.83
17	2	11	19.50	37.15	56.65
17	6	11	15.27	48.55	63.82
18	1	5	1.31	4.53	5.84
18	7	6	2.31	14.49	16.80
19	4	6	1.82	11.00	12.82
19	8	7	7.57	22.02	29.59
20	8	8	9.11	28.19	37.30
20	9	8	7.65	31.28	38.93

APPENDIX 9 Estimates of the dry weight of leaves and branch wood in the crowns of sample trees of *P. radiata* clone study

Tree number	Clone Number 546 A	579 A	582 A	602 A	605 A	954
Leaf Dry Weight (kg)						
1	4.36	4.91	3.82	3.34	12.25	2.02
2	1.90	2.38	1.49	3.66	4.24	2.82
3	3.85	4.54	2.85	4.40	6.84	1.56
4	2.39	3.88	2.30	4.32	3.15	2.33
5	6.34	2.93	1.59	1.85	3.97	1.41
6	3.18	4.47	3.35	3.31	6.32	1.47
7	4.76	3.14	2.91	3.28	4.21	0.80
8	4.55	3.25	1.36	1.61	3.38	2.33
9	1.98	2.18	2.04	0.50	4.86	1.07
10	1.54	2.81	2.16	3.03	6.25	0.44
11	1.43	2.73	2.16	5.64	2.34	0.30
12	2.21	1.28	1.34	1.46	9.79	0.72
13	1.67	2.11	0.79	1.21	4.75	2.59
14	3.46	5.41	0.61	1.46	2.22	0.34
15	2.56	4.86	1.25	1.24	2.21	0.69
16	2.31	2.30	1.25	3.03	2.24	0.57
17	1.42	2.10	1.87	1.57	2.89	1.59
18	0.73	1.32	1.28		1.84	1.31
19	1.28	0.80	1.93			0.62
20	3.58	2.45	1.62			0.59
Branch wood dry weight (kg)						
1	2.45	3.24	2.46	2.50	9.01	0.71
2	0.91	1.33	0.72	2.48	2.48	1.01
3	2.05	3.45	1.67	3.08	4.42	0.53
4	1.17	2.74	1.32	2.98	1.79	0.83
5	3.98	1.63	0.80	1.19	2.36	0.48
6	1.72	2.83	2.06	2.39	4.16	0.48
7	2.87	1.92	1.74	2.30	2.63	0.25
8	2.66	1.99	0.69	0.96	2.00	0.86
9	1.01	1.16	1.05	0.21	3.05	0.35
10	0.80	1.73	1.30	2.06	4.12	0.13
11	0.65	1.53	1.21	4.55	1.33	0.08
12	1.21	0.63	0.73	0.80	6.92	0.22
13	0.81	1.25	0.34	0.64	3.18	0.94
14	1.97	3.70	0.28	0.94	1.21	0.10
15	1.42	2.98	0.62	0.72	1.26	0.21
16	1.14	1.24	0.56	2.17	1.26	0.18
17	0.65	1.12	1.11	0.98	1.76	0.54
18	0.32	0.74	0.60		1.00	0.42
19	0.60	0.37	1.10			0.18
20	1.98	1.33	0.94			0.17

APPENDIX 10

Details of nutrient solution used in seedling study

Basic nutrient solution					
Nutrient salt	Volume of molar solution per litre of nutrient solution (ml)	Nutrient concentration in final nutrient solution (ppm)			
$Ca(No_3)_2.4H_2O$	2.5	Ca	100	N	70
KNO_3	1.5	K	59	N	21
$MgSO_4.7H_2O$	1.0	Mg	24	S	32
Micronutrients (prepared as combined solution)					
H_3BO_3	)			B	0.5
$MnSO_4.4H_2O$	)	Mn	0.25	S	0.15
$ZnSO_4.7H_2O$	)	Zn	0.07	S	0.03
$CuSO_4.5H_2O$	) 1.0	Cu	0.02	S	0.01
MoO_3	) (submolar)	Mo	0.01		
NaCl	)	Na	0.20	Cl	0.3
Fe- EDTA	1.0	Fe	0.5		
Treatment additions					
A. NH_4HPO_4	0.016	P	0.5	N	0.2
NH_4OH	0.98		-		13.7
B. NH_4HPO_4	0.050	P	1.5	N	0.7
NH_4OH	0.95		-		13.3
C. NH_4HPO_4	0.130	P	4.0	N	1.8
NH_4OH	0.87		-		12.2
D. NH_4HPO_4	0.260	P	8.0	N	3.6
NH_4OH	0.74		-		10.4

APPENDIX 11

Treatment means for *P. radiata* seedling experiment

Nutrient solution	Seedling batch							
	546A	582A	602A	605A	954 (1)	954 (2)	112A x BA21	MY 7 x CR 55
Top dry weight. (gm)								
A	0.669	0.547	0.550	0.494	0.600	0.554	0.580	0.642
B	0.928	0.611	0.645	0.594	0.629	0.633	0.745	0.725
C	0.799	0.671	0.782	0.719	0.702	0.692	0.621	0.803
D	0.581	0.580	0.619	0.526	0.592	0.588	0.525	0.752
Root dry weight (gm)								
A	0.151	0.108	0.138	0.081	0.134	0.134	0.129	0.144
B	0.170	0.106	0.131	0.076	0.136	0.128	0.146	0.116
C	0.120	0.115	0.155	0.092	0.151	0.162	0.124	0.135
D	0.075	0.112	0.131	0.087	0.159	0.158	0.110	0.118
Phosphorus content of tops (mg)								
A	0.822	0.760	0.680	0.556	0.879	0.640	0.838	0.710
B	2.122	1.448	1.590	1.172	1.629	1.677	2.253	1.828
C	2.004	1.981	2.510	2.239	2.058	1.848	2.077	2.152
D	1.918	1.951	1.863	1.329	2.283	2.000	1.683	2.296
Phosphorus content of roots (mg)								
A	0.360	0.258	0.439	0.245	0.406	0.681	0.623	0.372
B	0.561	0.463	0.439	0.281	0.602	1.126	1.206	0.678
C	0.730	0.525	0.648	0.389	0.297	0.318	0.354	0.852
D	0.668	0.707	0.716	0.626	0.488	0.532	0.652	1.192
Shoot : root dry weight ratio								
A	4.44	5.09	4.01	6.21	4.57	4.22	4.57	4.48
B	5.48	5.82	4.98	8.43	4.64	4.99	5.14	6.30
C	6.71	5.83	5.09	8.20	4.67	4.32	5.05	6.05
D	7.81	5.20	4.72	6.05	3.72	3.73	4.80	6.50